# Aspects of the Biology and Morphology of *Anisoplaca ptyoptera* Meyrick (Lepidoptera: Gelechiidae), a Potential Biological Control Agent of Gorse.

**A thesis submitted in partial fulfillment of the requirements for the Degree of Master of Applied Science**

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**Keywords:** *Anisoplaca ptyoptera*, Lepidoptera, Gelechiidae, biology, Carmichaelieae, *Carmichaelia*, gorse, *Ulex europaeus*, biological control, New Zealand, New Zealand endemic, new association.

*Anisoplaca ptyoptera* Meyrick (Lepidoptera: Gelechiidae) is a stem miner which attacks some members of the tribe Carmichaelieae (Fabaceae). Carmichaelieae and *A. ptyoptera* are both endemic to New Zealand. Recently it was noticed that the moth also attacks the exotic weed gorse (*Ulex europaeus* L.) (Butler 1979).

Larval feeding by *A. ptyoptera* structurally weakens the host and disrupts vascular transport; this causes dieback of branches, reduces flowering and growth and occasionally contributes to plant death. While various factors limit its potential in New Zealand, *A. ptyoptera* has been identified as a potentially useful insect in biological control programmes against gorse in Hawaii, Oregon and Chile.

A preliminary assessment of the suitability of *A. ptyoptera* as a biological control agent has been carried out in New Zealand. Aspects of the biology of *A. ptyoptera* on gorse have been investigated, the destruction of gorse by the moth in parts of Canterbury has been measured, the ease by which it can be artificially reared has been assessed, and techniques suitable for host specificity screening have been developed. Descriptions of *A. ptyoptera* adult and larva are also given.

The life history strategy of *A. ptyoptera* appears to be opportunistic univoltinism. The seasonal distribution of life stages is loosely synchronised. The possibility of diapause is discussed, although evidence of this is only slight. Adults emerge from late spring to autumn and larvae develop throughout the year. Thus damage to gorse continues throughout the entire growth and reproductive periods of gorse. Up to 94 percent of the mature plants at a site have been attacked. The loss of as much as 85 percent of foliage can be directly attributed to *A. ptyoptera* damage.

The mean potential fecundity is 196 eggs per female. The endemic population reaches high levels and is widespread, despite 33-49 percent parasitism of the larvae. Two undescribed species of larval parasitoid have been isolated: an endemic eulophid (*Zealachertus* sp.) and an ichneumonid (*Diadegma* sp.), which is probably also endemic. As these parasitoids appear to be restricted to New Zealand, the potential for *A. ptyoptera* to achieve high population levels outside New Zealand appears favourable.

The oligophagous feeding habits of *A. ptyoptera* necessitate a cautious approach to assessing its suitability as a biological control agent. Host specificity will be more thoroughly investigated in the 1989-1990 and 1990-1991 seasons. If an acceptable degree of specificity is found, there are excellent prospects for *A. ptyoptera* to make a significant contribution to biological control of gorse growing outside New Zealand.

**Reference:**

Butler, J.H.B. 1979. Control of gorse by *Anisoplaca ptyoptera. Proceedings of the 32nd New Zealand Weed and Pest Control Society Conference:* 307-8

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# *SECTION I: Introduction*

*Anisoplaca ptyoptera* Meyrick (Lepidoptera: Gelechiidae) is a stem miner that attacks some members of the tribe Carmichaelieae (Fabaceae). *A. ptyoptera* and Carmichaelieae (with one exception) are both endemic to New Zealand. In the early 1970s it was noticed that the moth had successfully colonised the exotic weed gorse (*Ulex europaeus* L.) (Butler 1979).

The damage to gorse foliage caused by *A. ptyoptera* larval feeding is very distinct. Larval feeding disrupts vascular transport in the stems of its host. This causes discolouration and die-back of the branches and also structurally weakens them. Occasionally *A. ptyoptera* attack contributes to the death of entire plants.

Gorse was introduced from north-west Europe to many countries because of its value as a fodder and hedge plant. Due to its aggressive invasion of agricultural and forestry land, gorse is now considered a serious weed in many places (Holm *et al.* 1979). As it is a weed more commonly associated with extensive land use, the control of gorse by conventional practices is economically limited. From the late 1920s, there has been a series of gorse biological control (= biocontrol) programmes (Hill 1982). The most comprehensive and prolific of these programmes is that currently being undertaken by the New Zealand Department of Scientific and Industrial Research (DSIR) Plant Protection's Biological Control of Weeds Section. As gorse biocontrol has gained momentum, the amount of available information related to it has grown.

The development of gorse biocontrol has perhaps mirrored the rising popularity of weed biocontrol in general (e.g., Julien 1987). Accompanying this rise has been the advance in the scientific basis of the discipline. Several recent publications have advocated the selection of weed biocontrol agents on the basis of their having various attributes (e.g., Goeden 1983; Wapshere 1985; Hokkanen 1986; Crawley 1986, 1989c; Lawton in press). The most controversial of these contributions has been the proposal of Hokkanen & Pimentel (1984, 1989) that "new associations" have a higher probability of delivering successful control than long evolved associations.

Biocontrol convention is to select agents from the fauna attacking the host in its place of origin. Contary to this convention, *A. ptyoptera* has been identified as a potentially useful insect in biocontrol programmes against gorse in Hawaii and possibly in Oregon and Chile.The potential of the moth in New Zealand is limited by i) the occurrence of parasitoids that attack it here; and ii) by the increased herbivore pressure the ancestral hosts may suffer because of an artificially increased or dispersed *A. ptyoptera* population.

As part of continuing co-operation between DSIR Plant Protection and the Hawaiian State Department of Agriculture, a project was conceived whereby the potential of *A. ptyoptera* as a gorse control agent is elucidated by examination of the moth in New Zealand. The initial part of this project was the work reported in this thesis.

The overall objective of the work in this thesis was to investigate the natural history of *A. ptyoptera* with an emphasis on the aspects that may affect to its potential as a biocontrol agent.

Specific aims within this objective have been to:
i) to determine the biology of *A. ptyoptera*;
ii) assess the damage it causes to gorse;
iii) develop techniques for any subsequent host specificity screening; and
iv) to describe the larva of *A. ptyoptera.*

Section II is a review of much of the information upon which the assessment of the biocontrol potential of *A. ptyoptera* rests. Section III deals with the larval description and instar analysis. In Section IV, some aspects of the biology of *A. ptyoptera* are discussed. These are: the seasonal distribution of life stages; larval feeding sites and behaviour; the incidence of parasitism; and fecundity and fertility.

Aspects which relate more exclusively to assessing a biocontrol candidate are addressed in Section V. These are: the damage characteristics of *A. ptyoptera*; the ease of culturing the moth; its host range and possible techniques specificit ; and the distribution of the moth.

Each sub-section contains a summary. The biology of *A. ptyoptera* is summarised and conclusions on its suitability as a biocontrol agent are drawn in Section VI.

# *SECTION II: Literature Review and Background Information*

## 2.1 Section Introduction

In this section, the background information and literature is drawn together to create the nucleus from which the subsequent sections are developed. Section 2.2 contains a review of the literature concerning *A. ptyoptera* including a brief summary of New Zealand Lepidoptera with a emphasis on the *Anisoplaca* genus. In addition the morphology of the *A. ptyoptera* adult is reviewed in detail. (The morphology of the larvae is described in section 3.1.) Section 2.3 is a brief review of the distribution, seasonality, natural enemies, pest status and control of gorse in New Zealand, Hawaii and Chile. Finally, a selective review of biocontrol principles is presented in Section 2.4. This review serves as a "knowledge base" for the investigations into the potential of *A. ptyoptera* as a biocontrol agent.

## 2.2 An Introduction to *A. ptyoptera*

Like most New Zealand insects, there has been very little literature published about *A. ptyoptera*. In this study, all the available information, published and unpublished, is compiled for the first time.

### 2.2.1 The Literature Concerning *A. ptyoptera*

The earliest literature on *Anisoplaca* was the description of the adult by Meyrick (1885a, b). This was followed by further descriptions by Philpott (1927) and Hudson (1928, 1939) (see Section 2.2.2).

Although *A. ptyoptera* was observed attacking gorse before 1972 (Plant Protection Centre MAF, correspondence file), information about this association was not published until 1979. Butler (1979) described the symptoms of damage to gorse caused by *A. ptyoptera* larval feeding and noted that this association was found at Rakaia Gorge and Leeston (both in Canterbury). He also discussed the likely importance of this insect as a control agent - noting the presence of parasites (then unknown) and the likely deleterious effect using this insect in New Zealand would have on the Carmichaelieae tribe. This present study is essentially the closer investigation into these areas that he called for.

MacCarter & Gaynor (1980) catalogued some of the insects attacking gorse in New Zealand, including *A. ptyoptera*. They too, described the damage caused by *A. ptyoptera* larval feeding, and pointed out that this moth is probably not a suitable candidate for gorse biocontrol in New Zealand. Ramsay et al. *(1988) suggested that A. ptyoptera* is one of the relatively few New Zealand insects species known to have successfully invaded an introduced plant.

Holder (in press) outlines various aspects of the moth's biology with reference to its use as a biocontrol agent outside New Zealand.

### 2.2.2 Taxonomy and Nomenclature

**Nomenclature**

| | |
|---|---|
| Order: | Lepidoptera |
| Sub Order | Ditrysia |
| Super Family: | Gelechoidea (*sensu* Common 1970) |
| Sub Family: | Gelechiidae (*sensu* Common 1970) |

*Anisoplaca ptyoptera*

The order Lepidoptera is the third largest in New Zealand (after Coleoptera and Diptera) with 1761 or so described species. Of these, 89.8 percent are endemic to New Zealand (Dugdale 1988). The order

Lepidoptera comprises 4 sub-orders; the primitive Zeugloptera, the Sachnonypha, the Monotrysia and the Ditrysia. Within the sub-order Ditrysia 26-28 super families are recognized. New Zealand has 11 of the 28 Ditrysian super-families recognized by Minet (1983) and Nielsen & Common (in prep. - cited in Dugdale 1988). Common (1970) and Nielsen & Common (in prep.) deal fairly extensively with the systematics of Lepidoptera to family level. Dugdale (1988) contains a key to family level of the lepidoptera found in New Zealand.

Within the super-family Gelechoidea, 18 genera are placed in the family Gelechiidae, 14 of which are represented in New Zealand. *Anisoplaca* is a small genus within the Gelechiidae family. Meyrick (1925), Philpott 1927 and Hudson 1928 reported that scattered members of the genus exist in South America, South Africa, Java and New Zealand. The accuracy of this statement has not been confirmed and the genus may be restricted to New Zealand. There are six species in the *Anisoplaca* genus including one undescribed species (*A. maculata* m.s.) (Dugdale 1988). There maybe another entity, although too few specimens of this have been collected to allow confirmation or dismissal of this possibility (Dugdale pers. comm.). *A. ptyoptera* is the type species of the genus (from original monotypy).

**Taxonomy of the Adult**

An alive *A. ptyoptera* adult is shown in the frontispiece.

Bulter (1979) incorrectly reported that the only published information on *A. ptyoptera* was a description of the adult by Hudson (1928). The original description was by Meyrick in 1885 (1885a and b) and is as follows. '*A. ptyoptera*, n.sp.*male* - 27mm. Head, thorax, and abdomen very pale whitish ochreous, shoulders narrowly dark fuscous. Palpi ochreous-whitish, basal half of second joint and a spot at base of terminal joint fuscous. Antennae fuscous. Legs pale whitish-ochreious, irrorated with dark fuscous. Forewings elongate, narrow, posteriorly somewhat dilated, apex obtuse, hingmargin hardly rounded, oblique; very pale whitish-ochreous, with a few blackish scales, and irregularly irrorated with grey except towards costa and apex, and on two round patches surrounding discal spots; costa irrorated with grey towards base; a black dot beneath costa at 1/4; three small black discal dots, first a 1.3, the other two transversely placed close together beyond middle: cilia ochreous-whitish, with a grey line, basal third suffusedly barred with grey. Hindwings light grey; cilia whitish, with a grey basal line.

Christchurch in March; one specimen received from Mr R.W. Fereday.' (Meyrick 1885b p.171)

Given that gorse was established throughout much of New Zealand by the 1880's, it is possible the monotype was from gorse, i.e., *A. ptyoptera* may have colonised gorse soon after the introduction of the plant in the mid 1800's, or any time up to the early 1970's - including repeated colonisations.

In 1928 Hudson also described the species: '*Anisoplaca ptyoptera*. This very remarkable looking species has occurred at Christchurch.

The expansion of the wings is 1 1/8 inches. The fore-wings are narrow-oblong with the termen almost straight; *dark ochreous-grey, with the veins clearly marked in pale greyish-ochreous;* there is a faint dot on the fold; *a conspicuous black discal dot at 1/3 and a double dot at 2/3, each being surrounded by a pale ring*. The hind-wings are dull greyish-ochreous with a fainter marginal band.

The perfect insect appears in February and March...' (Hudson 1928 p259, plate xxxviii., Fig. 1). Hudson (1938) added '*Anisoplaca ptyoptera* also from Mount Cook and Waiho Gorge.'

Philpott (1927) depicted the male genitalia of an *A. ptyoptera* specimen from Christchurch (p350 Fig. 2) and noted that it differs from *A. acrodactyla* and *A. achyrota* in that the shape of the harpes 'are more leaf-like and have a small tuft of stiff hairs on lower apical angle (sic)' (Philpott 1927 p349).

Dugdale (1988) catalogued the earlier authors noted above and gave the holotype information: 'Christchurch MC, R.W. Fereday; HT male unique, BM genitalia slide no.3796 male, BMNH.' He also recorded the six species in the genus.

## 2.3 Gorse: Distribution, Ecology and Pest Status

As part of the information needed to assess *A. ptyoptera* as a biocontrol agent, it is necessary to review some aspects of the target plant. The characteristics and history of gorse in Hawaii and Chile are reviewed because these countries are interested in introducting *A. ptyoptera*. Information regarding gorse in New Zealand is also reviewed because it is the place of *A. ptyoptera's* origin.

### 2.3.1 Taxonomy of Gorse

| | |
|---|---|
| Family: | Fabaceae (Syn. Leguminosae) |
| Sub-Family: | Faboideae (Syn. Papilionoideae) |
| Tribe: | Genisteae |
| | *Ulex europaeus* L. |

### 2.3.2 Introduction

Gorse (*Ulex europaeus* L.) is a thorny, perennial shrub in the sub-family Faboideae. It is a native of the Atlantic coast of western Europe and Great Britain. Gorse has been deliberately introducted to more than 15 countries or island groups around the world (Holm *et al.* 1979) outside western Europe. Gorse was introduced to many countries, including New Zealand, in the early 19th century because it was valued as an inexpensive, quick growing hedge and fodder crop (Moss 1960). However, gorse escaped from cultivation and has spread in almost every area it was introduced. It is now a weed in Australia (e.g., Wilson 1968), the Pacific north-west coast of mainland USA (Warren & Youngberg 1968), Chile (Norambuena *et al.* 1986), Hawaii (Markin *et al.* 1988) and New Zealand (e.g., Bascand 1973).

In New Zealand, the lack of natural enemies and the mild climate, combined with the agricultural practices of burning large areas of lowland forest and extensive grazing, proved ideal for gorse growth and dispersal. By 1859 gorse had become a serious weed in some parts of the country and in 1900 it was declared a noxious weed (Hackwell 1980). Gorse quickly became a pest in New Zealand and other temperate parts of the world due to its rapid distribution, its aggressive displacement of pasture and its ability to replace native vegetation and grasses on range land (Sandrey 1985; Hill 1986). It appears to be a plant of remarkable climatic adaptability.

In New Zealand gorse grows extremely quickly and annually produces 5-600 seeds/$m^2$ (Ivens 1978). The seeds can withstand burning and remain viable for over 30 years (MacCarter & Gaynor 1980). Clearing gorse results in rapid re-establishment from the massive seed bank (up to 20,000 seeds per $m^2$) and from regrowth of the old stumps.

In forestry land, gorse competes with seedlings of *Pinus radiata* and other tree species for nutrients and moisture, reducing first year stem diameter by 44 percent (Balneaves 1975). In addition, gorse impedes

pruning and planting operations. The most common forestry solution is burning or mechanical destruction combined with a multiple spray regime on the susceptible seedling and juvenile growth stages (Zabkiewicz & Balneaves 1984).

In agricultural land, gorse is an aggressive invader and competitor for pasture. It forms dense thickets that exclude stock and, once the long lived seed bank is established, removal and prevention of re-establishment of gorse is difficult. Recommended control involves: i) timed removal (burning or chemical); ii) oversow with a rapidly germinating pasture mixture; iii) fertilize (to enhance competitive ability of grasses); iv) high stocking; and v) follow-up spot treatment; chemical application, oversow, fertilize (MacCarter & Gaynor 1980).

However, as gorse is a weed problem usually associated with extensive agriculture and forestry, there are considerable economic restraints on the control methods that can be employed, since the increased costs (labour, fencing and chemical) will seldom be offset by increased production (Sandrey 1985).

The literature concerning the control methods available up to 1977 has been summarized and indexed in two bibliographies: Agriculture Research Council (1975) and Gaynor & MacCarter (1981). Zabkiewicz & Balneaves (1984) examined gorse control in New Zealand forestry.

Using goats to control gorse has been investigated by Radcliffe (1985, 1986, in press). MacCarter & Gaynor (1980), Hill (1986, 1987) and Hill & Gourlay (1989) discussed the history and future of biocontrol of gorse in New Zealand. The history of biocontrol to 1985 in Hawaii is reviewed by Funasaki *et al.* (1988) and Po-Yung Lai (1988), while biocontrol of gorse is discussed by Markin & Yoshioka (in press). Biocontrol in Chile prior to 1985 is reviewed and evaluated by Zuniga (1985). Norambuena *et al.* (1986) discussed the performance of *Apion ulicis* (Forster) (Coleoptera: Curculionidae) in Chile. No other literature concerning gorse biocontrol in Chile was found.

### 2.3.3 Distribution

The distribution centre of the genus *Ulex* appears to be northern Portugal. The genus contains 20 species (Bisby 1981), with three species occurring in northern Europe. Gorse is a native of western Europe (France, Great Britain, Portugal and Spain) (Tutin *et al.* 1967). Information regarding the identification and native distribution of gorse can be found in Tutin *et al.* (1967) and Clapham *et al.* (1987). The global distribution of gorse is given, along with a rank of importance in each country, in Holm *et al. (1979).*

*In New Zealand, gorse is found on more than 941 000 ha (Blaschke et al.* 1981), of which 166 000 ha has greater than 40 percent cover (Sandrey 1985). Gorse occurs in varying densities over much of New Zealand. In the South Island, gorse is present in all areas except Fiordland (areas for New Zealand follow those proposed by Crosby*et al.* 1976) (Bascand & Jowett 1981). The distribution of gorse in the North Island could not be determined. However, it is probably present in all areas where agriculture is practiced.

During 1984-87, Markin *et al.* (1988) investigated and described the distribution of gorse in Hawaii. It appears that gorse was introduced to the islands Maui and Hawaii sometime near the turn of the century. It is now naturalized on both these islands.

On the island of Hawaii, the infestation is restricted mainly to the south-east quadrant of Mauna Kea, between 450-2250 m altitude. The area of infestation on this island, not including isolated plants which possibly extend down the watershed into the forest reserves, has been estimated at 8262 ha. Most of the gorse is found in an inner block of continuous distribution covering 2509 ha (Markin *et al.* 1988).

On Maui, gorse is found in a primary infestation area on the north-east side of Red Hill on East Maui, roughly between the elevations 630 and 2220 m. In addition, there are isolated pockets of infestation on the north and east side of Red Hill. The total area of gorse infestation on Maui has been estimated to be 5985 ha. The area of continuous distribution is estimated to be between 517 ha (Markin *et al.* 1988) and 1227 ha (Markin & Yoshhioka in press).

### 2.3.4 Pest Status

As stated earlier, approximately 941 000 hectares of New Zealand is infested with gorse (Blaschke *et al.* 1981). It is arguably our most economically damaging weed. Annual costs of controlling gorse in agricultural and forestry land are at least NZ$22 million (Sandrey 1985). It has been estimated that land presently infested with gorse could yield between $NZ22 million (Sandrey 1985) and NZ$150 million (Monsanto 1984) in additional production per annum. A breakdown of the real and opportunity costs and the benefits accruing to gorse in New Zealand can be found in Sandrey (1985).

Despite intense efforts to control gorse, the area of infestation is probably increasing. Although it has not been nationally quantified, it appears that in the 1980s many gorse prone areas went under, or reverted to gorse infestation, as herbicide usage, grazing pressure and fertilizer application all decreased.

Currently, gorse in Hawaii is perceived as a 'range, forest and urban problem' (Markin & Yoshioka in prep.), but it is not a large economic problem. However the potential for the problem becoming extensive is great because of the extremely rapid growth and reproduction of the weed in Hawaii (Hill, pers. comm.) combined with the land uses and soil types on the islands.

On Maui, the infestation has apparently remained stable for the last 25 years, primarily due to continual control programmes by state agencies and local ranchers (Markin *et al.* 1988). However, the infestation is spreading down the watercourses, specifically Maliko Gulch, toward the sub-tropical forest areas and coast north of the primary infestation site (Yoshioka pers. comm.). There are further fears that as the area becomes subject to increasing development, vehicular transport will aid dispersal ot the weed to new areas.

On the island of Hawaii, although the present area of infestation is not great, the potential susceptible area of infestation is the whole eastern slope of Mauna Kea (Parker Ranch) (Hill pers. comm.). The extensive range land and open forest grazing practised in this region appears to be ideally suited for gorse. Indeed, gorse is advancing in a northerly direction from the present infestation site, and is expected to continue doing so unless containment measures are taken (Markin *et al.* 1988).

The extent of gorse infestation in Chile could not be determined. As in other places, gorse is one of Chile's principal weeds in forestry and agriculture (Norambuena *et al.* 1986). It invades areas important to these industries between latitudes 37 and 43 south (Osorio & Cerda 1984), a region typified by a Mediterranean climate (temperate/warm marine climate) (Norambuena *et al.* 1986).

As in New Zealand and Hawaii, the adaptive ability of this weed and the edaphic and climatic conditions of the region combined with the perennial life cycle, prolific seed production and absence of natural enemies of the weed (Norambuena *et al.* 1986), has allowed gorse to occupy extensive areas used for agriculture and forestry in Chile (Osorio & Cerda 1984). The economic impact of gorse in Chile was not determined.

### 2.3.5 Seasonality

In Great Britain, the seasonality of gorse is generally very regular: usually it flowers during spring and pods mature and dehisce in mid-summer. In mild winters, sporadic successful flowering and pod set can occur earlier than this (Hamilton 1980). All pods mature and dehisce in mid-summer (Hill 1982).

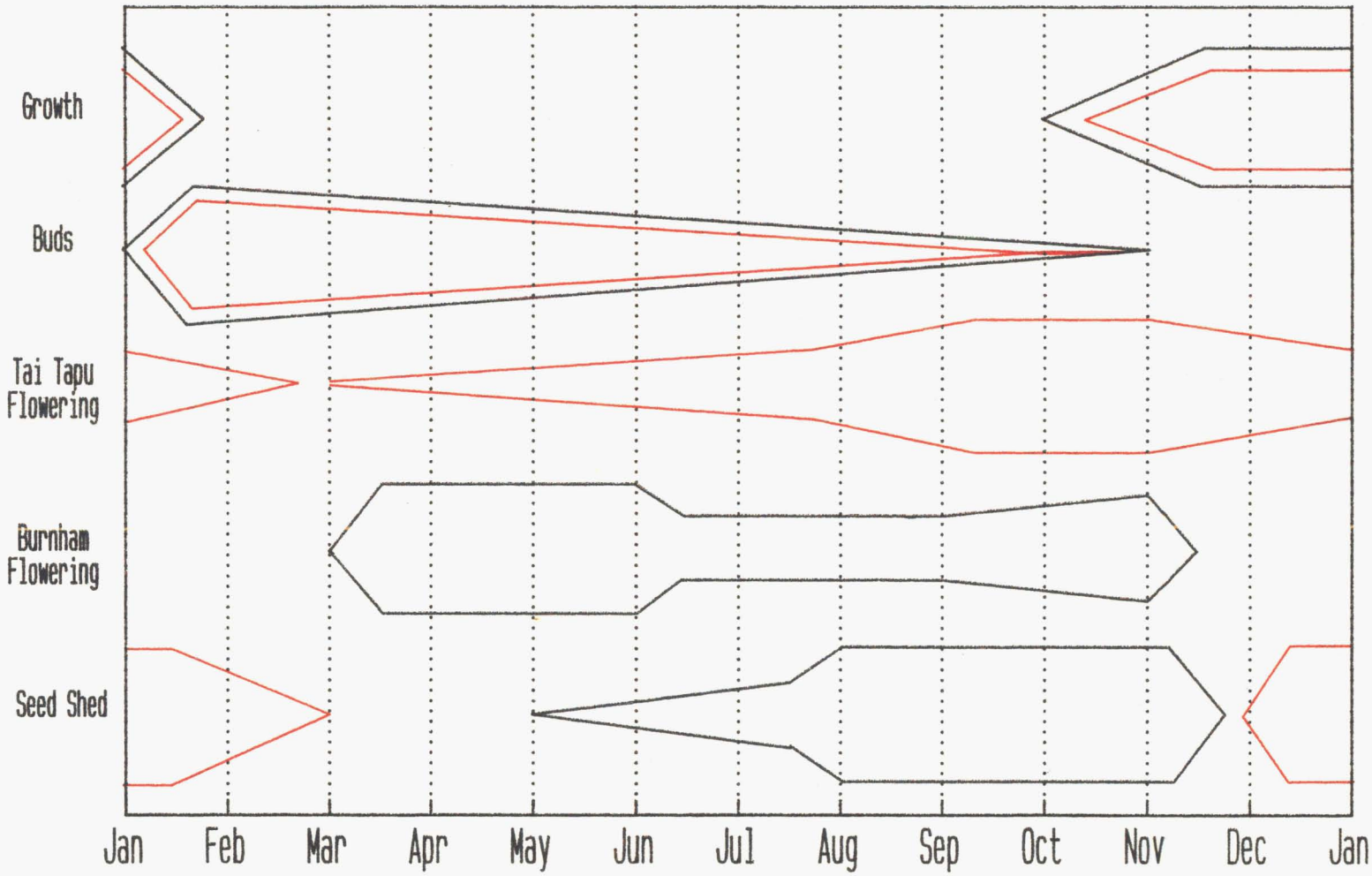
In contrast, the pattern of growth and reproductive periods of gorse in New Zealand are highly variable. This has led some authors to inaccurately propose that gorse sets seed twice each year (e.g., Cowley 1983; MacCarter & Gaynor 1980). Furthermore, Hackwell (1980) claimed that gorse flowered almost all year. However, gorse at higher latitudes and in southern New Zealand flowers almost exclusively in spring (Hill & Gourlay in prep.).

Gorse in New Zealand occupies a latitudinal range from 34 2' to 47 degrees South. It occurs from sea level to over 800 m altitude (MacCarter & Gaynor 1980). Given the wide climatic variation experienced, it is very difficult to accurately quantify the phenology of gorse throughout New Zealand.

Radcliffe (1986) and Hill & Gourlay (in prep.) have documented the seasonality of gorse in Canterbury. The seasonality of gorse at the sites used in this study is presented in Fig. 2.1. This indicates that gorse flowers and sheds seed only once a year, although Hill & Gourlay (in prep.) have shown that this can occur over an extended period.

In Hawaii, gorse begins flowering in early winter (November) and reaches maximum bloom in winter and spring (January to May). Flowering then tapers off in July with a low period in late summer and autumn

FIG. 2.1. The seasonal life history of gorse at two sites in Canterbury.
KEY: Black = Burnham; Red = Taitapu/Hoon Hay Valley



(August-October), yet flowers are never totally absent at any time of the year (Markin & Yoshioka in press).

The growth pattern of mature gorse comprises a burst of elongation from the tip of the current seasons growth followed by a period of hardening off. The following season, new shoots arise from the vegetative buds (cf. flower buds) in the axils of primary spines and stems which are protected by leaves (Hill 1982). These shoots elongate and harden and the pattern is continued. Thus separate seasons growth can usually be distinguished.

In New Zealand, the growth period of gorse typically starts in spring, peaks in early summer and finishes in summer. The tissue from this burst of elongation hardens off during summer before or as bud set begins. In Hawaii, the growth period begins in early spring, and the new growth hardens off during early summer. However, gorse in Hawaii has the remarkable ability to set flower and seed on the proximal end of a branch before the distal end has finished elongation and hardened off. This does not occur in New Zealand (Hill pers. comm.).

### 2.3.6 The Fauna of Weedy Gorse

This section outlines the faunal community attacking gorse in New Zealand, Hawaii and Chile so far as it could be determined.

In those areas of Europe with similar climate to New Zealand, gorse is rare because soil conditions, frost, agricultural practices and a complex of phytophagous organisms reduce its competitive capacity (Schroder & Zwolfer 1970).

In New Zealand, the level of natural control of gorse is low (MacCarter and Gaynor 1980), as it is in Hawaii (Markin & Yoshioka in press; Yoshioka pers. comm.) and Chile (Zuniga pers. comm.). The vertebrates that might control gorse in New Zealand (rabbits, goats, deer) are kept at low population levels and/or prefer more palatable foods (MacCarter & Gaynor 1980). On the island of Hawaii, sheep grazing is believed to have kept gorse in check until sheep were replaced with cattle in the 1950s. With minimal grazing on gorse by cattle the weed began to spread rapidly (Markin *et al.* 1988). The status and effect of gorse consuming vertebrates in Chile is unknown.

The fourteen arthropod species that have been found attacking gorse in New Zealand are shown in Table 2.1.

**TABLE 2.1: The arthropod fauna attacking gorse in New Zealand (modified from MacCarter & Gaynor 1980).**

| Animal | Order: Family | Structure attacked | Reference |
|---|---|---|---|
| *Anisoplaca ptyoptera* | Lepidoptera: Gelechiidae | stems | Butler (1979) |
| *Apion ulicis* | Coleoptera: Curculionidae | seeds | Miller (1970) |
| *Coccus hesperidum* | Hemiptera: Coccidae | spines | Anonymous (1971) |
| *Ditylenchus dipsaci* | Nematoda: Tylenchidae | stems | Hill and Gourlay (1989) |
| *Epiphyas postvittana* | Lepidoptera: Tortricidae | foliage | Thomas (1975) |
| *Eriophyes genistae* | Acari: Eriophyidae: | foliage | Hill and Gourlay (1989) |
| *Hemiberlesia rapax* | Hemiptera: Diaspididae | stems | Anonymous (1971) |
| *Icerya purchasi* | Hemiptera: Margarodidae | stems | Miller (1971) |
| *Lampides boeticus* | Lepidoptera: Lycinaedae | reproductives | Harding (1971) |
| *Oemona hirta* | Coleoptera: Cerambycidae | stems | Miller (1971) |
| *Parlatoria pittospori* | Hemiptera: Diaspididae | stems | Timlin (1964) |
| *Tetranychus lintearius* | Acari: Tetranychidae | foliage | Hill *et al.* (1989) |
| *Thrips obscuratus* | Thysanoptera: Thripidae | flowers | MacCarter & Gaynor (1980) |
| *Uresiphita polygonalis* | Lepidoptera: Pyralidae | foliage | Dugdale (pers. comm.) |

The following eight of these animals cause notable damage: *Epiphyas postvittana, Icerya purchasi, Oemona hirta, Ditylenchus dipsaci, Eriophyes genistae, Tetranychus lintearius, Apion ulicis* and *Anisoplaca ptyoptera. I. purchasi, O. hirta* and *Epiphyas postvittana* are horticultural pests and *D. dipsaci* is a pest to agriculture, so these animals can not be exploited for gorse control. *Eriophyes genistae* is a self introduced mite that has been recently recorded on gorse in New Zealand (Hill & Gourlay 1989). It appears widespread throughout much of New Zealand (Hill pers. comm.) and causes growth abnormalities in developing shoots (Gourlay pers. comm.). The effect of this mite on the vigour of gorse is unknown. Another mite, *Tetranychus lintearius*, was deliberately introduced and liberated as part of the DSIR Plant Protection gorse control programme in February 1989 (Hill *et al.* 1989). Feeding by this mite causes severe bronzing of gorse foliage and can kill entire plants (Hill 1987).

*Apion ulicis* was introduced to New Zealand in 1931 from England (near London) and is the only other agent that has been deliberately liberated for gorse control in New Zealand. The larvae of this weevil develop in the pod, feeding on the maturing seeds (Zwolfer 1962). The adults are liberated when the pod opens (MacCarter & Gaynor 1980). *A. ulicis* does not control gorse seed production in New Zealand as well as originally hoped. Sometimes only 70-80 percent of the pods from the summer flowering are infested (Hill pers. comm.) and because most of the pods from the autumn/winter flowering escape attack due to the (adult) weevil being in semi-diapause at this time (MacCarter & Gaynor 1980). Yet the programme has been at least partially successful (Classen 1978), and *A. ulicis* may have become one of our most common insects (Miller 1970), suggesting that other European agents for gorse control might flourish in New Zealand given the abundance of gorse, the favourable climate and lack of natural enemies.

*A. ptyoptera* is a stem boring moth which attacks some members of the tribe Carmichealieae (Faboideae) (see Section 5.4). Carmichealieae and *A. ptyoptera* are both endemic to New Zealand. Recently it was noticed that *A. ptyoptera* had successfully colonised gorse (Butler 1979). The larvae tunnel in the conductive tissues of the woody stems of its host (see Section 4.3). This causes die-back, reduced

flowering and growth and structurally weakens the host plant (see Section 5.2). The biology of *A. ptyoptera* and its potential effectiveness as a biocontrol agent are the subjects of this study.

Two factors limit the application of *A. ptyoptera* as a gorse control agent in New Zealand. Firstly, the native hosts (some of which are rare) might suffer if *A. ptyoptera* populations were encouraged artificially. Secondly, *A. ptyoptera* larvae suffer a high level of parasitism by parasitoids that are probably endemic (see Section 4. 4). Bulter (1979) and MacCarter & Gaynor (1980) proposed that local populations periodically crash due to this parasitism, leading to unsustained and sporadic gorse suppression.

Hence *A. ptyoptera* is appropriate for consideration as a biocontrol agent outside New Zealand, where the tribe Carmichealieae and the larval parasitoids appear not to exist (Holder in press).

The Nematoda and Arthropoda fauna attacking gorse in Hawaii is unknown to the author and appears not to have been documented. It is unknown if any of the Hawaiian endemic fauna attack gorse. The insect species imported into Hawaii for gorse control and their present status there are documented by Markin & Yoshioka (in press). Four insect species have been released and a further two are currently in quarantine and undergoing testing. Between 1926 and 1962 the following three species of *Apion* have been released: *A. ulicis*; the gall forming *A. scutellare* (Kirby); and an unidentified weevil, *Apion* sp. (possibly *uliciperda*). The strain of *A. ulicis* that is established in Hawaii originated in southern France (Hill pers. comm.). Unlike the strain present in New Zealand, the Hawaiian strain is thought to be multivoltine: adults are active year-round and eggs and feeding larvae can be found in green pods at all times (Markin & Yoshioka in press). However, the Hawaiian strain appears to be undergoing a population decline, possibly due to a (fungal?) pathogen (Hill pers. comm.)

*Agonopterix ulicetella* Stainton (Lepidoptera: Oecophoridae) was liberated in November 1988 (E. Yoshioka pers. comm.). The larvae of this moth feed on the green foliage of gorse and can defoliate plants entirely (Hill 1987). At the time of writing, *A. ulicetella* has been recovered (Hill pers. comm.), but because it has not undergone an Hawaiian winter, it has not achieved "established" status.

The two species currently in quarantine undergoing host specificity testing are the lace bug *Dictyonota strichnocera* (Hemiptera: Tingidae) and a foliage feeding thrip, *Sericothrips staphylinus* (Thysanoptera: Thripidae).

It is not known if all the natural enemies attacking gorse in Chile have been documented. At present, the Chilean gorse fauna appears to consist of three species: *Icerya purchasi* (Osorio & Cerda 1984); a tortricid moth *Proeulis trioueta* Obr. (probably a rare and an incidental association) (Zuniga pers. comm.) and the deliberately introduced *Apion ulicis* (Norambuena *et al.* 1986).

## 2.4 Biological Control

### 2.4.1 Introduction

This section contains a selected review of some of the principles of biocontrol. The principles of weed biocontrol (biocontrol using phytophagous insects) which are of relevance to this study (i.e., the initial assessment) are discussed. A comprehensive review of biocontrol in New Zealand up to 1987 can be found in Cameron *et al.* (1989).

Biocontrol is a broad term used to describe biological mortality agents lowering the size or vigour of a population. It is a naturally occurring phenomenon which is sometimes manipulated and applied by humanity to suppress pest populations.

Due to the problems associated with chemical pest suppression, there has been a surge in the interest and development of biological pest suppression during the last two decades. Biocontrol is a strategy that can be used on its own or in conjunction with other techniques of pest control. Besides prolonging the useful life of valuable chemicals, biocontrol has the additional advantages of being relatively cheap once established and usually not site specific.

Because biocontrol is a natural population process the target is not eliminated. Rather, the aim is to maintain the pest below the population level where the damage it causes is economically injurious, i.e., below the economic injury level (EIL). Ideally the target becomes rare.

Early biocontrol involved the importation of exotic insect species to suppress agricultural and horticultural insect and weed pests. By comparison, modern biocontrol investigates a much broader range of agents and targets, although biocontrol has remained largely the domain of entomologists. There are several possible reasons for this, including:
i) the wide diversity of insects, making the range of potential agents large;
ii) insects are humans' greatest competitors in areas of health and food supply (Southwood 1977); and
iii) entomologists have been used for biological control programmes in favour of specialists from other fields (Harris 1973).

### 2.4.2 Evaluation Systems and Desirable Characteristics of Biological Control Agents

'The success of any pest control programme depends on a combination of its effectiveness and its cost' (Harris 1984). Undertaking a biocontrol programme is an expensive and time consuming exercise (Harris 1973, 1979). Therefore, a great deal of emphasis is placed on ensuring that the most appropriate agents are chosen and the selection process is efficient (e.g. Harris 1973; Wapshere 1974c; Huffaker 1978; Goeden 1983; Müller in press and references therein).

When evaluating candidate agents, there is a broad range of criteria that can be used. The particular criteria used by an agency will be determined by the nature and circumstances of the target and candidate agent. Each programme is unique and thus the factors relevant to one may be less important to another (Sands & Harley 1981; Hokkanen 1986). However, it should be noted the biocontrol principles from which these criteria are derived are, in the main, poorly understood generalisations that often lack empirical support (Lawton in press). The basic reasons for the eventual success or failure of a programme may thus be poorly understood, and so the evaluation criteria used can only provide general guidelines (van den Bosch *et al.* 1982; Wapshere 1985).

### 2.4.2.1 Scoring Systems

In the arena of weed biocontrol, many systems have been proposed in an attempt to increase the chances of selecting successful agents (e.g., Harris 1973; Frick 1974; Wapshere 1975, 1985; Goeden 1977, 1983; Winder & Harley 1978). Harris (1973) proposed a weighted scoring system which considered a range of properties that seemed to influence the eventual outcome, i.e., desirable and undesirable characters incorporated into a single score. Goeden (1983) modified Harris's system so that the characteristics of a candidate are scored in a triple tiered system. The criteria of the first tier include the extent and timing of the damage caused by the candidate and its ability to reproduced. Measures of risk and ease of culture form the second tier. Ecoclimatic similarity and other estimates of a candidate's potential effectiveness in the area of introduction constitute the third.

In retrospect, the scoring systems of Harris and Goeden have limitations and omissions and use inappropriate criteria. One obvious limitation of these systems is that they simplify and generalise (Goeden 1983). However, their principal limitation is probably the need to use predictions and guesses inherent in making an assessment before the candidate has been liberated. Thus, these systems are reported to be difficult and awkward to use as intended, i.e., before host specificity screening has begun (Lawton in press).

One important omission the current scoring systems make is that they do not consider plant population dynamics (Crawley 1989a; Müller in press). To make predictions on how insect herbivory will affect plant abundance it is necessary to know the key factors acting at each stage in the plant's life cycle and which, if any, of these factors act in a density dependent manner (Crawley 1989a). Unfortunately, there is very little information concerning the effects of insect attack on plant population dynamics.

Julien (1987) catalogued all recorded weed biocontrol efforts up to 1985 and their status. Recent analysis of the Julien data (Lawton in press) and a similar data set (the Silwood project on the biological control of weeds (Moran 1985)) by Crawley (1989b, c), reveal another omission of scoring systems in that the order to which the candidate belongs is not considered. Although the effect of taxonomic group is not great, Diptera and Lepidoptera appear less likely to become established and less likely to provide effective control than Coleoptera and Hemiptera.

On the other hand, some of the assumptions included in scoring systems have little scientific basis. For example, the general belief that phytophages which attack vascular or support tissues have greatest potential as weed biocontrol agents and gall formers and leaf miners the least, does not appear to be supported (Lawton in press). There is no clear relationship between mode of attack and success as a weed biocontrol agent (Hokkanen 1986; Crawley 1989a,c).

Although the scoring approaches do have limitations, the above criticisms allow further modification of Harris's and Goeden's scoring systems. Although the systems are subjective and difficult to use as intended, they do provide a format for evaluating candidate agents which otherwise does not exist. However, because of the shortcomings of these systems, a candidate should not be abandoned simply because it scores badly. The criteria considered in the evaluation of *A. ptyoptera* in this study are primarily the criteria advocated by Goeden (1983).

Wapshere (1985) proposed another system for determining priorities among candidate agents. This system is simpler than those of Harris and Goeden, and places greater emphasis on ecoclimatic matching between the place of origin and the proposed release site (Wapshere 1970, 1975). In this system, agents which reduce weed populations in regions ecoclimatically equivalent to the infested regions receive first priority for further study. This system also has difficulties, such as quantifying the impact of agents (Müller in press) and lack of evidence supporting average climatic mismatching as a major cause of failure to establish (Crawley 1986, 1987) (but see discussion in Section 2.4.2.1).

In summary, there is a large number of biological and ecological mechanisms that affect biocontrol agents, and their operation is complex. Many characteristics are advocated as desirable, but the workings of most of them are not understood at present (Harris 1984). Empirical investigation of the fundamental principles involved would probably advance biocontrol greatly (Lawton in press).

Predictive systems suffer inaccuracies because of this complexity and the absence of a knowledge base. However, they do represent an interpretation of our current knowledge, and provide a format for evaluation which otherwise might not exist. There is no magic formula for selecting biocontrol agents.

#### 2.4.2.2 Desirable characteristics

The characteristics that appear to contribute to an agents success or ability to establish are discussed in the following list. This list is rather exhaustive and some of the criteria are desirable rather than essential. In addition, many of the criteria are interrelated and difficult to separate.

1) **"Nothing succeeds like success"** (Crawley 1989c). Perhaps the most common approach to biological weed control is to select agents with a proven track record (Julien *et al.* 1984). This makes good sense, as agents with a previous record of successful control appear to have a greater probability of successful of control elsewhere (Harris, preface in Julien 1982; Crawley 1989c). In addition, using previously used

agents is relatively inexpensive because most of the pre-release studies required will have been done (Harris 1984) or can be done co-operatively.

2) **Similar ecoclimatic tolerances to that of the target.** Matching of climate is believed to improve the chances of a biocontrol organism becoming established (see discussion below; Wapshere 1970, 1975, 1985; Hokkanen 1986). In addition, it has been proposed that if target and agent have similar environmental tolerances, the agent will be effective throughout the host's range (Coppel & Mertins 1977).

3) **High levels of damage.** Intuitively, it appears wise to select agents which have the most obvious impact on the target. Goeden (1983) proposed that agents which destroyed vascular or support tissues or destroyed the seeds of annuals (or biennials) are most desirable. This may be the case, but a not entirely exclusive theory of damage threshold, proposed by Harris (1981a), states that all damage inflicted counts and may accumulate and several agents may collectively push the weed over some stress threshold and cause decline. Further, there is no clear relationship between mode of attack and success as a weed biocontrol agent (Crawley 1989a; Hokkanen 1986).

Harris (1984) suggested that it might be more useful to rate biocontrol agents in terms of the proportion of the annual production removed or destroyed. Crawley (1989a), in a review of the literature concerning the effect of herbivores on plant population dynamics, suggested that a knowledge of how an agent will effect the target plant population dynamics is necessary to make value judgements. However, both of the above approaches are likely to be too expensive or time consuming to be useful in many pre-liberation assessments.

4) **Prolonged attack phenology.** Agents which damage the weed at the most critical phase in its phenology or make it susceptible to decline through frost, drought, competition or subsequent attack, are desirable. Agents which attack over a prolonged period over the entire growth season (or reproductive period, especially of annuals) are most desirable (Goeden 1983). For this reason, multivoltine agents are traditionally considered more desirable than univoltine candidates because it is assumed that the former have longer periods of attack (Harris 1973; Goeden 1983) . However, some univoltine insects also have long feeding periods, possibly due to prolonged oviposition and/or emergence (Harris 1973).

However, it is rare to find an agent which is individually very damaging and which attacks its host over a prolonged period (Wapshere 1985). More frequently a combination of phenologically or habitat complementary agents are selected (Hill pers. comm.). If synchronisation of agent attack and target susceptibility does not occur naturally, it may be artificially achieved by inoculative release (small numbers for medium term and local control) or inundative release (large numbers for short term control) of natural enemies (Stehr 1982).

5) **Ability to respond to host density.** Ideally a biocontrol agent can initially control a large host population and later respond quickly to changes in host numbers to prohibit outbreaks (Huffaker & Kennett

1966; Huffaker *et al.* 1977). Coppel & Mertins (1977) proposed that this ability is largely dependent on a strong and rapid "numerical response" to density (*sensu* Solomon 1949). This is, in turn, dependent on several other characteristics:

i) High reproductive capacity relative to the host (Krebs 1978). In addition to increasing the probability of establishment, features associated with high intrinsic rates of increase (i.e., small body size, short generation time and high fecundity) also tend to favour more effective weed control (Crawley 1986; Lawton in press). In contrast, Goeden (1983) believed body weight (size) is irreleyant to performance but favoured high fecundity and multivolinism. Wapshere (1985) proposed that high fecundity reflects a high risk life-style (at least for eggs and early stages) (e.g., Tallamy & Denno 1981) and suggested that repoductive ability is therefore neutral.

ii) **A good searching capacity** may enable natural enemies to exert control at low target densities (and therefore maintain the pest at that level) (Huffaker *et al.* 1977). Yet the debate on host plant location and the influence of host plant density is a melting-pot of considerable theorising but little empirical evidence (e.g., Root 1973; Kareiva 1983; Stanton 1983). Consequently the searching capacity *per se* of biocontrol candidates is generally not assessed.

iii) **Good dispersal capacity.** Ideally, an agent will rapidly expand its sphere of influence to match that of the target. The agent's ability to do so is related to its searching capacity and ecological tolerance. Harris (1973) and Goeden (1983) employed the distribution of the candidate in relation to the range of the weed as a measure of ecological tolerance and adaptability. Their rankings agree with the more recent findings of Bergelson & Crawley (1989 - cited in Crawley 1989c); the most successful agents appear to be those that are widespread and abundant in their place of origin. Therefore attention should be paid to ensuring genetic variation in an agent population, especially given that weeds are typically highly polymorphic and adaptable and occur in a wide variety of places (Winder & Harley 1978).

6) **Host Specificity.** Because of the danger to crop plants, ornamentals and the endemic flora, host specificity is the critical criterion in evaluating exotic phytophages in weed biocontrol programmes. Unless a candidate feeds only on the target, it is unlikely to be released (Crawley 1989b).

Paradoxically, Harris (1973) gives oligophagy a high score and restricted monophagy a low score a measure of the low degree of host-parasite homeostasis that has been proposed to be desirable (see Pimmentel 1963). However, oligophagy implies that the candidate occurs on several hosts. Goeden (1983) suggested that Harris had put too much emphasis on using agents from plants related to the weed and not enough on the necessity that the agent be well adapted to dealing with the weed species. For in successful weed biocontrol projects, the agents are often very highly, if not completely, host specific (Andres & Goeden 1971; DeBach 1974).

Alternatively, a positive implication of oligophagy may be that the agent is able to use another host species while the primary target is unavailable. The release of an oliogophagous agent would only be permissible if the alternative hosts were also weeds.

7) **Relative immunity to non specific enemies.** To maximise the reproductive potential of biocontrol agents, they are liberated after being freed of their associated natural enemies by rigorous quarantine procedures (Huffaker 1957; Harris 1971; Frick 1974).

Despite these efforts, mortality due to resident natural enemies is often the reason why agents imported for weed biocontrol fail to establish, or if they establish, have never achieved regulatory densities (Remmington 1968; Goeden & Louda 1976) (see Section 4.5 for discussion). Of the natural enemies responsible, generalist predators are the most important (especially egg eating ants) (Crawley 1986, 1987), being cited as responsible in about twice as many failures as parasitoids (Lawton in press). Parasitoids are in turn significantly more important than disease (Lawton 1986, Crawley 1986). Recent studies of native natural enemies attacking introduced weed biocontrol agents include Nuessly & Goeden (1983, 1984), Briese (1986a) and Goeden *et al.* (1987).

8) **Ability to be artificially reared.** If the agent is easily cultured then host specificity determination, quarantine procedures and rearing large numbers for release is greatly facilitated (Goeden 1983) (artificial rearing is discussed in Section 5.3). Conversely, the inability to be artificially reared does not necessarily preclude an agent from undergoing testing, quarantine and liberation, but these procedures are then more difficult and complicated (e.g., field tests).

Additional desirable criteria may be:
9) **field hardiness;**
10) **persistence;**
11) **social acceptability.** This can determine the availability of funding for a project; and
12) **relative inexpense (and reliability)** (Samways 1981).

### 2.4.3 Biological Control Strategies

Amid various definitions, the four categories or strategies of weed biocontrol currently recognized are: i) "classical"/ inoculative; ii) inundative/ augmentive; iii) conservative; and iv) broad spectrum (Wapshere *et al.* 1985).

#### 2.4.3.1 "Classical" Biological Control

Classical biocontrol is the regulation of a pest by deliberate importation and release of an exotic natural enemy of the target species. An agent is liberated only after stringent host specificity testing and quarantine precautions are taken (Harris 1971). Frequently the pest is an introduced species which has achieved pest status in its new natural enemy free and/or climatically favourable environment (Caltagirone 1981). The introduction of host specific phytophagous insects, minus their own natural enemies, should theoretically reduce the abundance of the alien weed in a typical host-enemy interaction (DeBach 1964; Andres &

Goeden 1971; Frick 1974). An often cited example of classical weed biocontrol is the control of prickly pear (*Opuntia* spp.) in Australia primarily by the Argentine moth, *Cactoblastis cactorum* (Berg.) (Holloway 1964).

The successful contol of *Icerya purchasi* in Californian citrus crops by *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae) (Doutt 1964; Claussen 1978; Caltagirone & Doutt 1989) led to a period in which many insects were collected from all over the world and released in North America without any host testing or quarantine precautions. Because of repeated failure this dangerous policy was stopped (Turnbull & Chant 1961). However from these early irresponsible failures, the need for sound understanding of the biology of both pest and control agent (through research) was realized, and a systematic method of locating, testing and releasing biocontrol candidates has been established (see section 2.4.4) (Waage & Greathead 1988).

Classical biocontrol was the earliest strategy of weed biocontrol to be practised (Holloway 1964). It has generally proven to be the most economical and probably the most successful of all the weed biocontrol strategies (Batra 1981) and is the most commonly used biocontrol method (Hokkanen 1986). The positive attributes of classical weed biocontrol (note that many of these attributes also apply to other forms of biocontrol) include:

i) **permanence:** if the agent becomes established the effects are persistent;

ii) **environmental safety:** there are no residues or pollution from weed biocontrol, although the ecological effects on the native biota are not always considered (Johnson 1985; Pemberton 1985);

iii) **specificity;**

iv) **responsiveness:** ideally, an agent can disperse itself to, and respond to, all suitable habitats where the weed exists (Delfosse & Cullen 1985);

v) **cost effectiveness:** although the initial outlay may be considerable (Harris 1979), once the agent is established costs are non-recurrent. Further, for successful programmes there is a high benefit:cost ratio (Marsden *et al.* 1980), and the ratio of success and the cost of classical biocontrol are likely to be at least as good as the strike rate and expense in the search for new pesticides (Lawton pers. comm.).

However, weed biocontrol does have several disadvantages. Perhaps the germ of all disadvantages is our lack of knowledge; as a rule, we do not know the basic reasons why biocontrol does or does not work (Krebs 1978). As a result we have few or no predictive theories (Crawley 1987) and most introductions are trial and error. Acquiring knowledge is made difficult by the complexity of interacting critical features and the relative importance of each factor being different for each particular biocontrol situation (Hokkanen 1986).

Frequently discussed disadvantages of biocontrol include the following.

i) **The high initial outlay** of time, effort and money (Combellack 1989); up to US$2m (Harris 1979) and 15-20 years (Batra 1982).

ii) **The high rate of failure**; results are not guaranteed. Of the 1128 insect releases made against weeds (Julien 1987) for which the outcome can be classified, only about 30 (Lawton in press) to 40% (Julien *et al.* 1984) of programmes initiated are successful (partial to good control). However, given that the samples are not independent (i.e., same agent or same target) and consistent measures of success are difficult to define in biocontrol programmes (Harris 1985; Greathead 1986), there is more than one possible result from the Julien list data, thus the results should be interpreted carefully.

iii) **Biological control is relatively slow acting** (Frick 1974), and its effectiveness varies with the local situation (Delfosse & Cullen 1985).

iv) **Conflicts of interests** arise because the effect is not localised (Huffaker 1978). The weight of economic, ecological and/or political interests are generally used to solve such conflicts (Harris 1985), but complete resolution is not always possible (Andres 1981).

v) **Danger to non-target species:** Importing phytophagous agents involves taking calculated risks. Several authors have discussed the risk of host transference, and discounted it because of the adaptations and absolute requirements specialist insects have for their host (Huffaker 1957, 1962; Harris & Zwolfer 1968; Zwolfer & Harris 1971; Frick 1974; Dunn 1978; Lawton 1985; CABI 1986). However, the probability of an unexpected host shift is not zero (Lawton 1985; see Section 5.4.3.3) and at least one situation exists where an weed biocontrol insect caused economic damage (Davies & Greathead 1967).

vi) **Inability to control several weed species in disturbed/unstable environments (e.g., annual crops)** because of the specificity of the agents and the result not being immeadiate (Frick 1974; Batra 1982; Delfosse & Cullen 1985).

vii) The effectiveness of weed biocontrol agents is often diminished by other methods of weed control.

viii) The advantages of classical weed biocontrol do not accrue to individual growers. Consequently, there is little incentive for the private sector to fund or develop biocontrol, and most biocontrol research is carried out by universities and government sponsored organisations. This may limit the development of the science (Samways 1981).

### 2.4.3.2 Other Strategies in Weed Biocontrol

**Inundative weed biocontrol** usually involves mass production and periodic release of native natural enemies against native weeds (Batra 1982; Delfosse & Cullen 1985). The theory of this process lies in increasing the local abundance, and therefore effectiveness, of the natural enemies in a region (Knipling 1977). This strategy is a technological response (cf. ecological) to a weed problem where maintaining a reservoir of natural enemies might be difficult, e.g., in annual or other unstable crop ecosystems (Batra 1982). Given the expense and difficulties associated with mass rearing and releasing large numbers of insects (Morrison & King 1977), fungi appear to be the favoured agents and in entomophagous programmes a trend is emerging away from inundative methods towards carefully timed inoculative methods (Waage & Greathead 1988).

**Conservation of natural enemies** in weed biocontrol may involve reducing antagonists of the agent or promoting the agent through habitat modification (Batra 1982). This strategy applies primarily to control

of native weeds by manipulation of native natural enemies (Frick 1974) and is, as yet, largely a theoretical and unproven concept (Delfosse & Cullen 1985). However, conservation biocontrol for arthropod control is achieved through several cultural methods and is a traditional method of reducing pests in many places (Batra 1982).

**Broad spectrum weed biocontrol** involves employing polyphagous agents to attack all weeds in a region. Most cases of this strategy against terrestrial weeds involve the manipulation of large vertebrate grazers such as cattle, goats, geese, etc. (Delfosse & Cullen 1985).

### 2.4.4 Executing a Classical Biocontrol Programme

As the science of biocontrol has developed, general guidelines for undertaking a novel biocontrol programme have emerged. In general these are followed, taking into account the unique circumstances of each biocontrol situation.

#### 2.4.4.1 Searching for Natural Enemies

Once it has been decided to attempt biological control of an exotic weed, the initial phase is to undertake two surveys:
i) an extensive review of the literature and knowledge pertaining to the target weed (Schroeder 1983), including information concerning taxonomic position, biology, ecology, economic importance, geographic distributions (including probable the centre of origin), and known natural enemies (National Academy of Sciences 1968; Frick 1974); and
ii) a survey to determine what insects are already present on the target locally and the extent of their damage (Goeden 1977).

On the basis of the above information, one or more geographical regions are chosen for a survey of the target plant (and sometimes of related plants) and the natural enemies associated with these plants (Frick 1974; Schroeder & Goeden 1986). Wapshere (1975, 1985) stressed that the key to finding the most effective natural enemies is searching in regions which are ecoclimatically homologous to the proposed site of introduction. Alternatively, it may be more fruitful to search in the region of the weed's adaptive centre of origin (Vavilov 1949/50), as this area is likely to contain the greatest diversity of natural enemies (DeBach 1964; Harris 1971) as well as the most specialised enemies (Wapshere 1974d). Perhaps the regions where these two areas overlap will be the most fruitful area of search.

Although climatic matching appears intuitively "right" and is followed to a certain extent by most biocontrol workers (Lawton in press), strict adherence to this principle is now questioned. For, although extreme events can destroy vulnerable founding populations, there is no evidence to support the theory that average climatic matching increases the probability of establishment (Crawley 1986, 1987). Indeed, liberating a biocontrol agent in a less extreme climate may improve the probability of establishment

(Lawton in press) and success (Huffaker *et al.* 1976). Nevertheless, it is almost certain that at least reasonable climatic matching is crucial. The lack of evidence to the contrary is probably due to most releases being made with good to reasonable climatic matching and climatically mismatched "test cases" being insufficiently documented.

The identification of the target, close relatives and the natural enemies encountered, rests on sound taxonomic knowledge and skills (Kilgore & Doutt 1967; DeBach 1964, 1974; Harris 1984). Using these skills, a list of natural enemies attacking the plant is compiled. The identity of these species and other appropriate information is usually gathered by conducting field surveys of the weed (and sometimes its relatives) (Wapshere 1974b). This is usually necessary because the literature concerning host plants and their phytophagous arthropods is generally incomplete and often unreliable (Harris & Zwolfer 1968; Zwolfer & Harris 1971).

The criteria discussed in section 2.4.2 are used to assess the members of the list of natural enemies, and a priority list is established. Detailed studies of the biology and host range of the more promising agents are then undertaken.

#### 2.4.4.2 Quarantine and Host Range Testing

If a biocontrol candidate is to be exported, it is subjected to vigorous host specificity testing. It is generally more efficient to do this in the country of origin where quarantine facilities are not needed. The aim of phytophagous host specificity screening is to determine the candidate's breadth of diet. Because of the risk to non-target plants, a great deal of emphasis is placed on the specificity or "safety" of potential imports and this is the most severe restriction in approving the importation and liberation of an agent (Crawley 1989b). Consequently, the body of literature on this topic is extensive (e.g., Harris & Zwolfer 1968; Zwolfer & Harris 1971; Wapshere 1974a, b, d; Dunn 1978; Cullen in press).

Early researchers developed the starvation test, where an insect is given the choice of starving to death or feeding on non-host test plants, and the negative oviposition test, which examines the ability of gravid females to oviposite on plants other than the target. As the science of host specificity developed, these "negative attack" tests were strongly criticized as yielding information of limited biological meaning (e.g., Harris & Zwolfer 1968; Dunn 1978; Martinat & Barbosa 1987). In natural situations, hunger is likely to be a stimulus for dispersal (Miller & Strickler 1983), whereas in the enclosed starvation test situation, many phytophagous insects will feed or oviposit on anything rather than starve or not lay (Crawley 1983). As a result many false positives are produced that are likely to have little relevance to real world host discrimination and which indicate a wider host range than actually occurs (Force 1966; Frick & Andres 1967; Dunn 1978). As a result, the data obtained from starvation tests are often difficult to interpret.

Nevertheless, starvation tests are still relied on, for they can be carried out in quarantine conditions and they do delimit a physiologically possible host range (Cullen in press). Therefore starvation tests allow the many plant species which the candidate fails to feed on to be removed from further consideration.

Frick (1970) described a multiple plant starvation test. There are varying designs on this theme, but the common principle is the presence of the normal host at the same time as the test plant (i.e., "choice test"). As choice is an integral aspect of an insect's behaviour under natural conditions, choice tests will almost always allow a closer estimation of the likely host range (Cullen in press). Caution must also be exercised in the interpretation of choice tests because i) the presence of non-hosts can influence the insect's ability to distinguish its host plant; and ii) choice tests do not reproduce choice as it operates in the field (i.e., when the host is rare or absent) (Dunn 1978; Cullen in press).

The biological relevance of host specificity screening is also dependent on the test plants the candidate agent is tested against. Amid varying designs and combinations there are four main methods that have been advocated to determine host specificity. These are briefly outlined below.

i) Early biocontrol researchers tended to rely on the "crop testing method". In this method a wide range of economically important plants, not necessarily related to the weed, are exposed to the candidate. This method yields information of little value: logistical constraints limit the number of species able to be tested, and although the species tested are shown to be safe from attack, there is no certainty that one or more of the untested plants will not be attacked (Harris & Zwolfer 1968; Wapshere 1974c).

ii) Harris & Zwolfer (1968) proposed a more positive method, where the candidate's actual host range is determined using a series of investigations that attempt to elucidate the agent's adapted features (physiological, morphological, phenological, ecological, ethological, chemical) that ensure host specificity. This method is impractical because the determination of physiological, ecological and ethological specializations are, in generally, beyond our present understanding (Wapshere 1974b).

iii) Frick (1970) developed a method of delimiting an insect's host range by testing the agent against a series of plants phylogenetically related to the weed.

iv) Wapshere (1974a, b, 1975) championed the phylogenetic testing method of Frick, developing the "centrifugal phylogenetic" method of selecting test plants. In this method, a sequence from the plants most closely related to the weed progressing through to more distantly related plants are exposed to the candidate agent, until the host range is delimited. To this sequence a "safety net" of further test plants (largely drawn from Harris & Zwolfer (1968)) is added, in which the range of test plants is extended to include:

a) cultivated plants botanically related to the host;

b) host plants of insects closely related to the candidate insect;

c) plant from which the candidate agent has been previously recorded;

d) plants on which little entomological work has been done; and

e) economically important plants which have evolved apart from the agent and have not been previously exposed to it.

f) In addition, Harris & Zwolfer (1968) suggested that plants with morphological or biochemical characters similar to those of the target should also be tested.

The centrifugal phylogenetic technique and its associated safety net or variations thereof is the contemporary method of selecting test plants in weed biocontrol. However, it should be pointed out that there is no absolute test to determine host specificity (Zwolfer and Harris 1971), therefore the final estimate of an insect's specificity in the field is partly a matter of judgement. Assessment appears to rely on a combination of good information, a good understanding of the ecological context of host specific biology and behaviour (Lawton 1985), a certain amount of experimental improvisation and careful interpretation (see Harris 1985).

Appropriate design of specificity tests and interpretation of the results require a broad understanding of interactions between the candidate and its host plant (Harris 1985; Schroeder & Goeden 1986).

If the export of an candidate is approved, the candidate is also screened to minimise hyperparasites and disease. Once the culture reaches its destination it is kept and reared in a quarantine laboratory and subjected to more rigorous screening for "hyper-enemies" and to eliminate contaminating non-candidate organisms which might reduce the effectiveness of control or increase the risk of non-target attack (Frick 1974).

#### 2.4.4.3 Classical Biocontrol Agent Liberation and Establishment

If a candidate species is believed to be "safe" and has undergone quarantine screening then a population, usually of limited numbers is prepared for liberation in the field. It is generally assumed that, if possible, insect introductions should involve obtaining and maintaining a large gene pool in the culture and liberating a genetically diverse population (e.g., Remmington 1968; Marshall *et al.* 1981; Joslyn 1984).

The concept of sub-specific geographical variation in animals is generally accepted (Mayr 1947) and, as Sands & Harley (1981) pointed out, different genotypes of an agent have different behavioural and physiological responses which are likely to limit the effective range of tolerance in each genotype.

Variability in an insect culture is best obtained by collecting individuals from many sites over the species' range (Remmington 1968; Van den Bosch 1971; McDonald 1976; Winder & Harley 1978; Marshall *et al.* 1981). Further, Remmington (1968) suggested maximising genetic variability by introducing "a large, wild sample from a large, central source population..." (although this practice is limited by quarantine considerations) and Myers & Sabath (1981) suggested the best sources of biocontrol agents 'are from expanding populations...', because of the increased genetic variance alleged to exist in these populations.

Although the above practices are theoretically sound, recent studies have been unable to demonstrate that genetic considerations actually contribute to biocontrol success (Myers & Sabath 1981; Ehler & Andres 1983). (However, in attempting to test the genetic diversity principle, it would be extremely difficult to separate the effects of reproductive potential (r), taxonomy, etc. and this has presumably not been

attempted.) Other studies suggest that genetic variation may even be deleterious. For example, a cross between two strains of a species can result in reduced fitness in the progeny (cf. parents) (Force 1967, Legner 1972, Bregliano *et al.* 1980).

However, empirical evidence may be drawn from the observation of Crawley (1987): that agents that are widespread and abundant (in their native land) are more likely to establish than rare, local species. Although it is uncertain whether wide geographic tolerance reflects genetic/ecological tolerance and flexibility (Brown 1984) or is caused by associated physical features (body size, maybe r) (Gaston & Lawton 1988).

The theoretically desirable considerations aside, practical problems of executing biocontrol are considerable and the theoretical aspects are often not given full consideration (Schroeder & Goeden 1986). Collecting rare natural enemies, usually from limited geographical areas, often results in genetically small samples (Messenger & van den Bosch 1971; Sands & Harley 1981), but rearing the agents in the laboratory, often on artificial media, is probably the most detrimental pre-release aspect of biocontrol (Myers & Sabath 1981). Insectory propagation of agents is usually necessary for quarantine procedures and to provide adequate numbers for release in the target area. This may, however, reduce the genetic variability of the culture and create directional selection for survival in insectory conditions, resulting in reduced fitness (Boller 1972; Mackauer 1972, 1981; Ashley *et al.* 1973). Some procedures for reducing quality loss are outlined by Mackauer (1981).

Another aspect which is important in the execution of biocontrol programmes is the number of individuals released. The probability of establishment is markedly enhanced by making large releases (Beirne 1975; Ehler & Hall 1982 - although these studies refer to entomophagous releases), presumably because large releases favour rapid build-up of populations, lessening the chances of extinction (Lawton in press). Hokkanen (1986) suggested that large releases also influence the genetic diversity within the colonizing population, which they may well do. An alternative to a single release is making several sequential releases ("multiple releases"). This appears to increase the rate of establishment and success in weed control programmes (Julien *et al.* 1984).

# *SECTION III: The Larva: Larval Description and Instar Analysis*

In this section aspects that are concerned with the larvae are investigated.

## 3.1 Description, Setal map, and Diagnostic Characters of the *Anisoplaca ptyoptera* Larva

A description of the larvae is not related to the biology of *A. ptyoptera* nor is it traditionally part of the assessment of a biocontrol candidate. Yet taxonomic precision is an accutely important aspect of any biocontrol effort (Kilgore & Doutt 1967; DeBach 1964, 1974; Harris 1984). The adult life stage of *A. ptyoptera* has been adequately described (see Section 2.2.2) but, perhaps not surprisingly, a published description of the immature stages of *A. ptyoptera* does not exist. Given the potential economic importance of this moth, an attempt has been made to describe the distinguishing characteristics of the larva in the following section.

### 3.1.1 Methods of Study

The equipment used to examine the larvae was a Leitz stereoscopic microscope fitted with an eye-piece grid or micrometer as required, and a Schott halogen optical fibre lamp (KL1500). Fine jewellers' forceps (INOX #5) and fine probes were used to manipulate the larvae. Circon iris scissors were used to dissect larvae.

When collected, larvae were fixed in Carnoy's fluid (recipe given in Appendix I) for 24 hours then transferred to 70 percent alcohol for storage. Only mature larvae (deemed to be in the last instar) were used for examination and description.

In the main, the areas examined in this part of the study followed the principles developed by MacKay (1959, 1962) and Peterson (1962).

Whole mounts of specimens were used for depicting the head, the 10th abdominal segment (A10), and the A6 abdominal proleg. The lateral surface of the head was examined by dissecting the head from the body and mounting it in Heinz mounting medium (see Appendix I) on a convex slide. The specimens examined for depicting A10, the A6 abdominal proleg, and the dorsal and ventral views of the head, were examined in 70 percent alcohol.

To observe the setae and pinacula of the body, transparent preparations of the integument were made using the technique of MacKay (1959, 1962): the larva was slit dorsally using iris scissors, then the body contents were removed by heating it in a 10 percent potassium hydroxide solution (KOH) for 10-15 minutes. The integument was then thoroughly washed and mounted on a microscope slide in Heinz mounting medium.

To observe the labrum, the head was dissected and its contents removed by heating it in 10 percent KOH. The head was then washed in water and stained in Chlorozol black E. (see Appendix I). The labrum was then dissected from the head and mounted in a 50 percent glycerol solution.

The relative positions and sizes of the setae and other structures on the head, A10 and the A6 abdominal proleg are depicted in three dimensional representations of these segments. The arrangement of the setae and pinacula on the segments T1, 2, A1, 2, 6, 7, 8, 9 are shown in a two dimensional setal map. By convention, the arrangement on the left hand side of the body is shown (Stehr 1987).

Many different systems of setal nomenclature have been proposed. The more influential (and well known) of these systems appear to be those of Dyar (1894, 1896), Forbes (1910), Fracker (1915), Heinrich (1916), Gerasimov (1935), Hinton (1946) and Mutuura (1956). Some of the various systems have been reviewed by Hinton (1946) and Stehr (1987) and others.

The nomenclatorial system proposed by Stehr (1987) (based on Hinton 1946) is used here for labelling the setae and pinacula. The pores on the prothoracic (T1) shield are labelled using the system of Hinton (1946). The various pigmented markings on the T1 shield are labelled using the terminology of Mutuura (1980) as simplified by Stehr & Neunzig (1981). The nomenclature proposed by Matsuda (1965) was used in this study for labelling the mouth parts. The nomenclature applied to the setae and structures of the labrum followed that of Steinmann & Zombori (1984) (after Peterson 1962).

### 3.1.2 General Introduction

Stehr (1987) provided a (limited) key to the family level using larval characteristics. In addition, he documented information on family diagnoses and descriptions of family characters.

Owing to the size of the Gelechioidea superfamily and the diversity and variation among its larvae, a satisfactory family key is not possible with our present knowledge. In fact, distinction between some gelechiids and members of the families Cosmospterigidae and Oecophoridae is not currently possible (Stehr 1987). However, certain characters and combinations of characters can help to define gelechiid larvae, even though some of these characters may, in isolation, occur in some species of other families. Several of these gelechiid characters and character combinations are given in Stehr (1987 p394).

Similarly, while the structure and features of *A. ptyoptera* may not be distinctive or diagnostic, the character of some features combined with (more common) family traits may project a distinguishable image.

The occurrence of features typical of powerful wood-boring larvae is a prevalent theme in the larval structure of *A. ptyoptera*. Further, features which may be used to separate *A. ptyoptera* from other members of the *Anisoplaca* genus include:

i) the hosts of *A. ptyoptera* are all in the sub-family Faboidae (see Section 5.4) whereas the other *Anisoplaca* members are restricted to the genera *Plagianthus*, *Hibiscus* and *Hoheria* that are in the Malvaceae family;
ii) *A. ptyoptera* is the only true "stemborer" in the genus, although some of the other genus members can be found in twigs (Dugdale pers. comm.); and
iii) *A. ptyoptera* adults are much larger than the other *Anisoplaca* members.

### 3.1.3 General Description

The larvae of *A. ptyoptera* appear to generally conform to the plan of Gelechiidae given in Stehr (1987), Hodges (1966, 1983) and Peterson (1962).

The mature larvae of *A. ptyoptera* that were examined ranged in length from 15.5 to 26 mm. The average length was 19 mm, which is large for gelechiids (cf. Peterson 1962 and Stehr 1987).

The head capsule is uniformly (no stripes) moderately to heavily pigmented (depending on age since last moult). The body is a uniform yellow-cream colour. The setal pinacula are light brown and are usually distinct, especially so for the dorsal pinacula. The pinacula are progressively less pigmented from dorsal to ventral.

Cuticular spinules are present. Generally, they occur uniformly on the non-sclerotised areas of the skin, but they also occur on a few sclerotised regions. The spinules are small and dense, but not minute; they are apparent at 32x magnification and can be observed at any magnification over 72x (using a transparent preparation). The spinules are conically shaped and slightly darker than the body colour (see Fig. 3.4).

Spiracles are lightly sclerotised and distinct. They are oval, except for the A8 spiracle which is circular. T1 and A8 spiracles are larger than A1-7 spiracles (by one and a half times or more).

Similar to stem boring cerambycid larvae, *A. ptyoptera* is characterised by the prothorax being larger (both wider and deeper) than the other segments of the thorax. This is diagnostic for *A. ptyoptera* (Dugdale pers. comm.). Also the segments T1, 2, 3, A1, 2, 3(?) usually become sequentially narrower.

Other Lepidoptera larvae one is liable to find in gorse in New Zealand are: *Barea* sp. (Oecophoridae); *Izatha peroneanella* Walker (Oecophoridae); *Phaeosaces apocrypta* Meyrick (Oecophoridae); and *Erechthias fulguritella* (Walk.) (Tineidae). The above larvae are able to to distinguished from *A. ptyoptera* by the following.
i) They will not have the swollen thorax and strong oral frame of *A. ptyoptera*, although the oecophorids are in the Gelechiodea and hence their chetataxy will be similar.
ii) *E. fulguritella* is a tineid and has a reduced number of functional occelli and L1, L2 on separate pinacula.
iii) None of the species in the above list feed on living gorse tissue (Dugdale pers. comm.).

**FIG. 3.1: Dorsal-frontal view of the head-capsule of *A. ptyoptera* larvae showing the arrangement of the primary setae, the pores and the stemmata.**

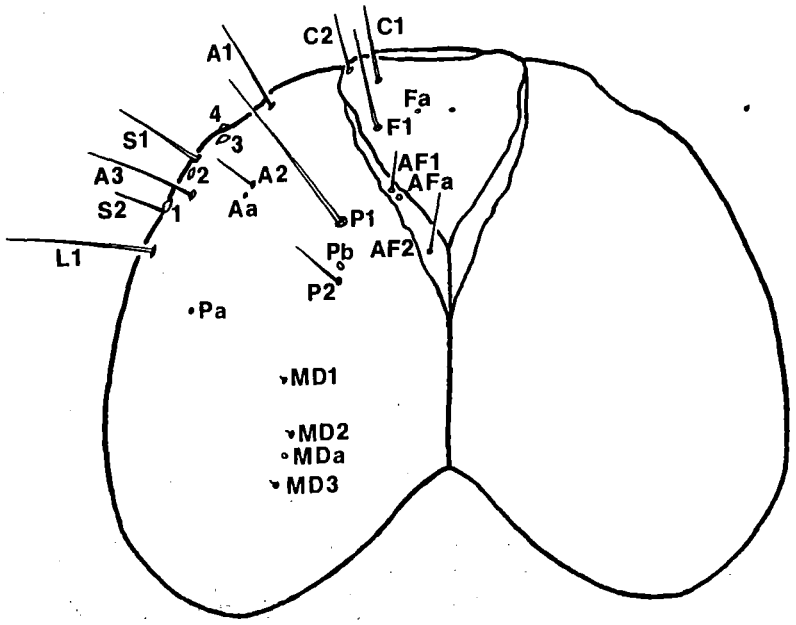



**FIG. 3.2: The arrangement of the primary setae, the pores and the stemmata on the head-capsule of *A. ptyoptera* larvae. Lateral view**

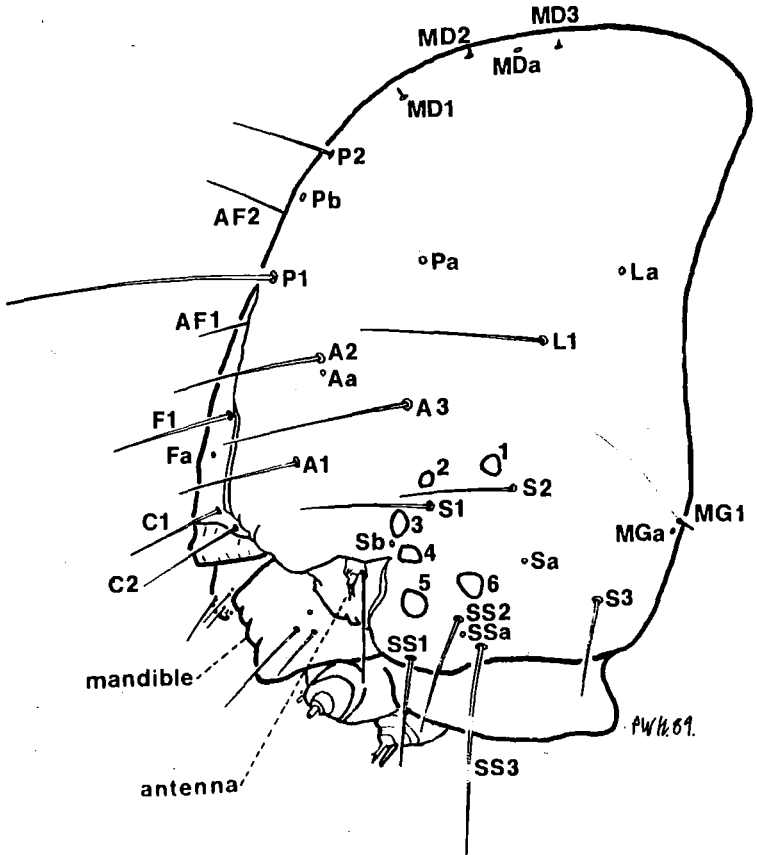


**FIG. 3.3: The arrangement of the primary setae, the pores and the stemmata on the head-capsule of *A. ptyoptera* larvae. Ventral view**

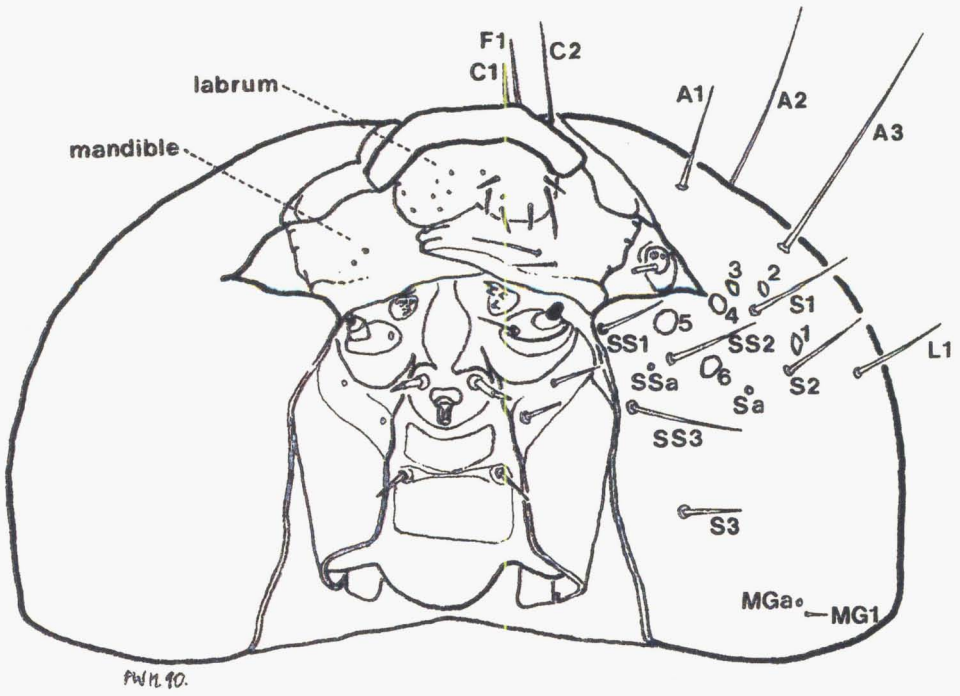
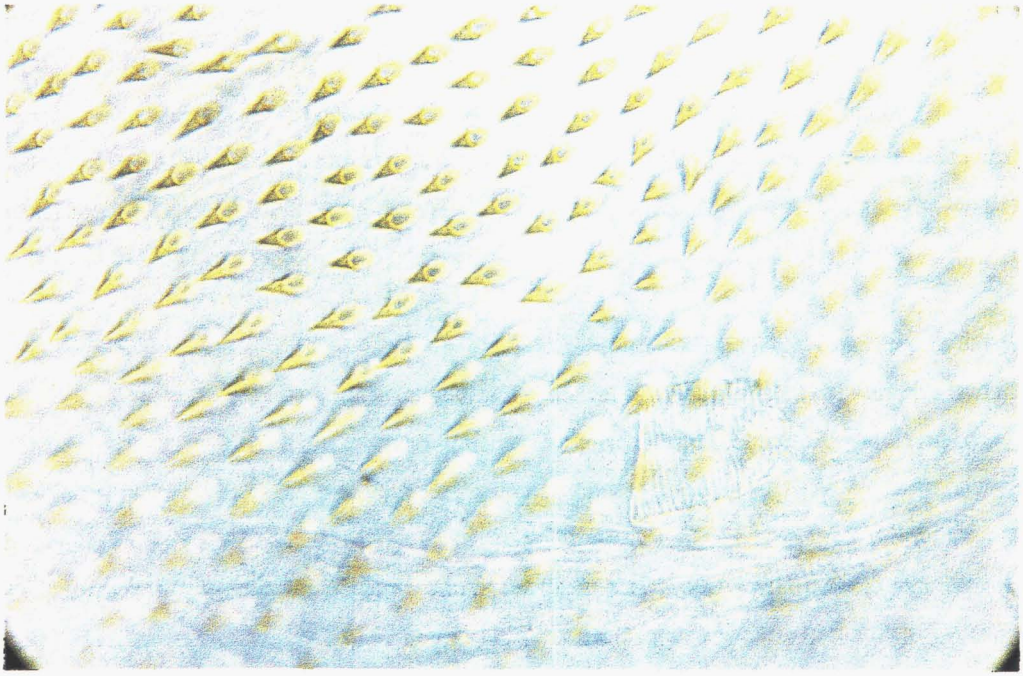



**FIG. 3.4: The detail of the integument of a *A. ptyoptera* larva viewed using a transparent preparation. The spinnules are conically shaped and slightly darker than the body colour. They are small and dense but not minute. They can be observed at any magnification over 72x using a transparent preparation.**



**HEAD**

The head-capsule is smooth and held obliquely (semihypognathous). The suture between the frons and clypeus is indistinct. The anteclypeus is translucent and protuberant. The thickening of the region around the oral region is common in wood-boring larvae. A feature of *A. ptyoptera* is a heavily sclerotised region around the labrum and mandibles which forms a thickened "oral frame". This is visible in the ventral view of head (Fig. 3.3). Given the toughness of gorse (Hill 1982), presumably the thickened oral frame serves as a point of attachment for the necessarily powerful mandibular muscles.

The arrangement of the primary setae, the pores and the stemmata of the head is given in Figures 3.1, 3.2, 3.3. The stemmata are arranged in an uneven arc: stemmata 1, 2 & 3 are distributed in a slight curve; 3 & 4 are close together with 4 lying adjacent to the 'corner' of the "antennal pit"; stemmata 4, 5 & 6 are distributed in a triangle with 5 lying low on the "face". The chaetotaxy of the head appears to be typical of most gelechiids (cf. Stehr 1987), including the distance between L1 and A3 being greater than the distance between A3 and A2. Possible distinguishing features include: i) MG1 is posterior to MGa and both MGa and MG1 are more posterio-lateral than typical; and ii) SSa is closer to SS2 than to SS3. The position of MDa is variable in its spatial relationship to MD2 and MD3. An additional pore (Ab?) was observed posterio-lateral to A2 in one specimen (out of 12 examined).

The labrum has the typical complement (Steinmann & Zombori 1984) of six setal pairs. The arrangement of setae is shown in Fig. 3.5a & 3.3 (note the right hand side is depicted in Fig 3.5a). There are two pairs of pores on the labrum. The more distinct of the pores is situated between seta labralis medialis secunda (in the sense of Peterson 1962) and SLM tertia; the other is above and toward the centreline from SLM prima (see Fig. 3.5a). The epipharynx (labrum, ventral view) has three pairs of paleae sensillum styloconicum. The arrangement and shape of the paleae is shown in Fig. 3.5b. The dorsal surface of the labrum has a sparse uneven coat of minute, very slender spinules.

An "in-situ" view of the mandibles is shown in Figures 3.2, 3.3 & 3.6. There is a small pore dorsal to the two mandibular setae. The "teeth" are distinct (see Fig. 3.6) but may become blunt in older larvae. Unfortunately, detailed examination of the mandibles was not carried out. Given that the mandibles are the source of many features used in sub-family identification (Stehr 1987), a more thorough examination of this structure may have been appropriate.

As part of the stem-boring theme, the antennae of *A. ptyoptera* are reduced and largely recessed in the triangle-shaped area adjacent to the base of the mandibles (its protuberance has been over emphasised in Fig. 3.2). The antennae often appears to be two-segmented because the first segment is small and largely obscured. Segment two is cylindrical and much larger than segments one & three. The arrangement of the sense organs arising from the distal ends of segments two and three are depicted in Fig. 3.7 - the 'long hair' (sensillum trichodeum) arises from the posterior end of the distal part of segment two. Segment three is very reduced and arises on the anterior end of segment two, flanked by two sensilla basiconica. Arising

**FIG. 3.5a: The arrangement of setae and pores on the labrum of an *A. ptyoptera* larva. Note the presence of two pores.**

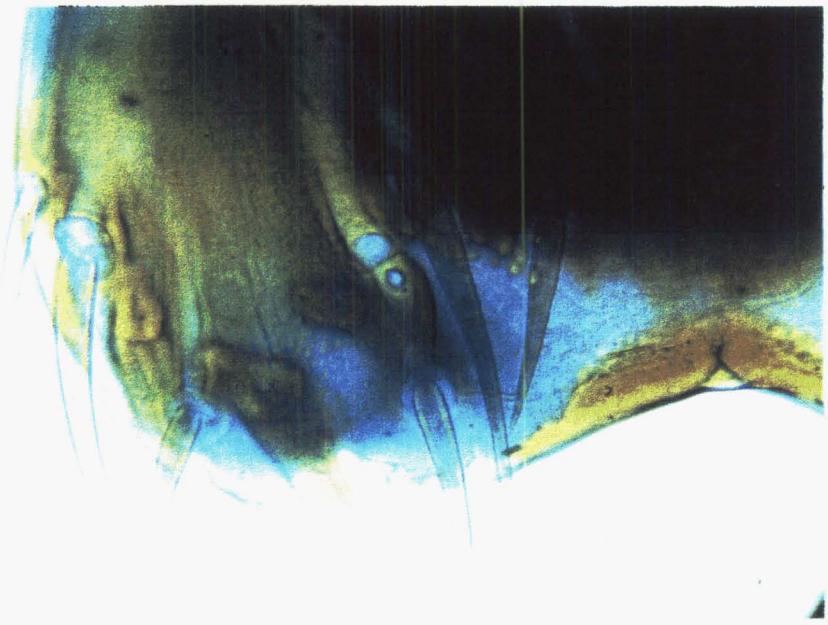


**FIG. 3.5b: View of the epipharynx of an *A. ptyoptera* larva, showing the paleae sensillum styloconicum**

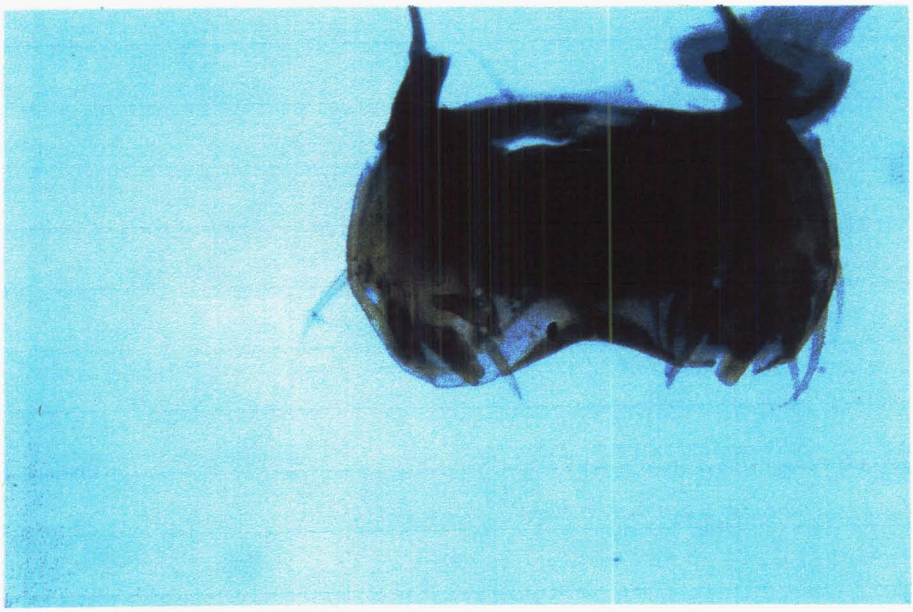


**FIG. 3.6: Frontal-ventral view of the oral region of an *A. ptyoptera* larva. Note the distinct "teeth" on the mandibles.**

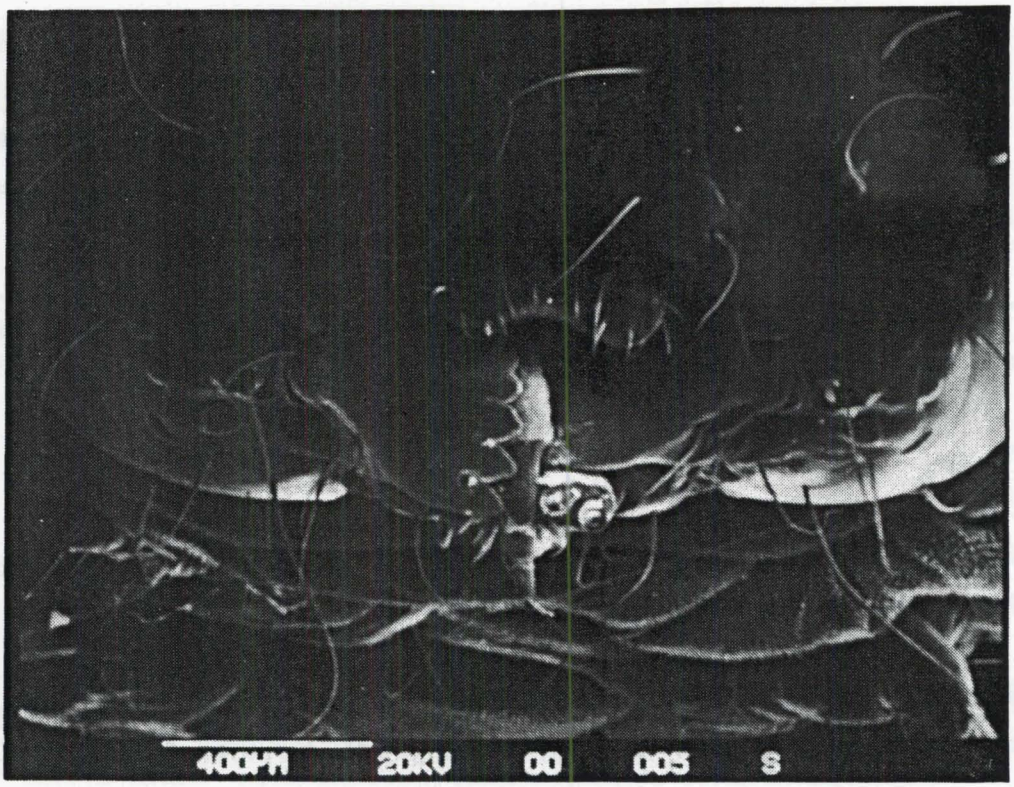
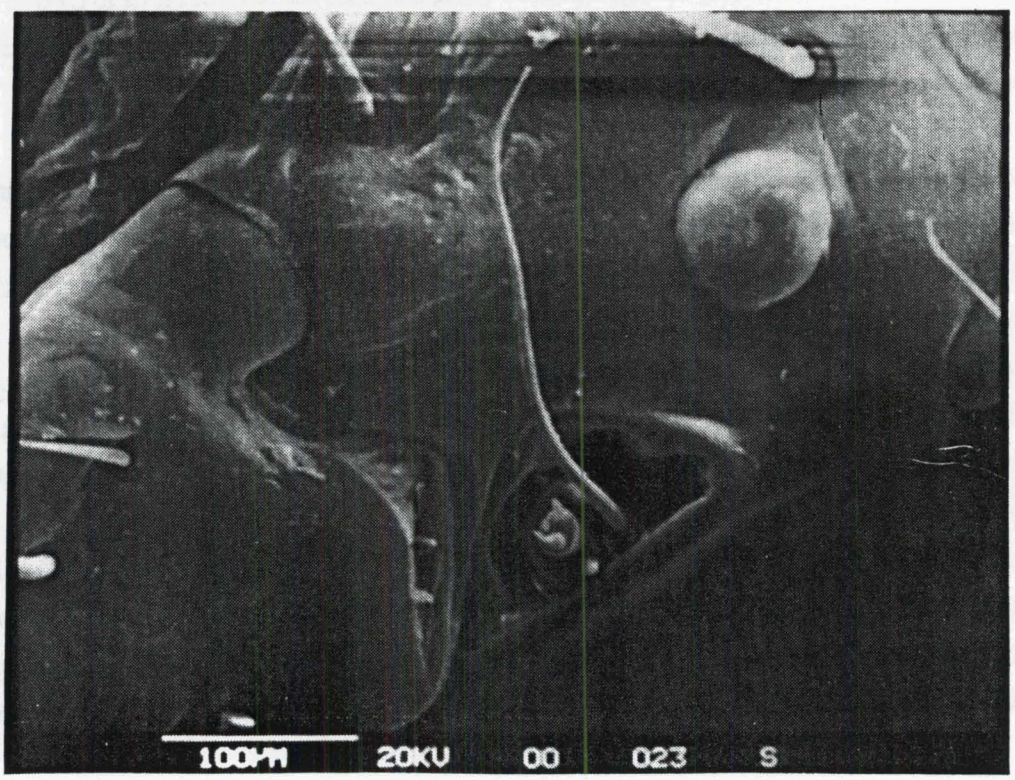



**FIG. 3.7: Detail of an *A. ptyoptera* larva's antenna. The antennae are reduced and largely recessed in the "antennal pit."**



from the distal end of segment three, there appears to be another sensillum basiconicum, a pair of small sensilla basiconica (close together) and a relatively large sensillum styloconicum.

The structure of the maxillary palpus is shown in Fig 3.8. The maxillary palpi are two segmented, which conforms to the typical arrangement (Matsuda 1965). On the terminal segment are six minute sensillae. Also situated on the stipes are the galea, lacinia, sensillum trichoduem and five other setae. These structures are too small to be clearly viewed with a stereoscopic microscope. Their structure and orientation also is shown in Fig. 3.8.

The spinneret and labial palpi are shown in Fig. 3.9. The labial palpi have three segments with a sensillum arising from the top anterior end of the second and third segments.

**Thorax**

As mentioned earlier, T1 is wider and deeper than T2 and T3. This appears to be a characteristic of *A. ptyoptera* (Dugdale pers. comm.).

The arrangement of setae on the thorax and abdomen is shown in Fig. 3.10. T1 appears to have a standard complement of setae except that the L group is sometimes reduced to two setae on one side.

Stehr (1987) reported that the middle setae of the L group (L1) on T1 is 'usually distinctly lower' in gelechiids. This is not the case in *A. ptyoptera*; L2, L1 & L3 of T1 are approximately in a straight line.

T2 and T3 have setae normally arranged with SV being unisetose and with L1 closer to L2 than to L3. A possible sub-family distinguishing feature may be the size of the pinacula of the L group - the L3 pinacula on T2 is very large for one seta.

Mutuura (1980) proposed that the pigmented spots ("tonofibrillary platelets") found at muscle attachments on the sclerotised parts of the integument can be a useful taxonomic character in larval classification. Stehr & Neunzig (1981) and Stehr (1987) supported the validity of using tonofibrillary platelets for classification below the family level in some taxa (as does the work of Gaskin (1975a p350) in his revision of the New Zealand Crambini). Hence the pigmentation pattern of the T1 shield of *A. ptyoptera* may be a distinguishing feature. Adjacent to seta D2 is a cluster of variably pigmented, often overlapping spots, the arrangement of which is shown in Fig. 3.11. These spots appear to fall into two rough groupings. The most dorsal group - possibly TP TIFA 1 or TP TIC 3 - consists of four spots and is immediately anterior of seta D2. The more lateral group, TP TIFA 2, is ventral to D2 and has five spots. Although the depth of pigmentation of these spots is variable, they were regularly placed in the different specimens examined. In addition to these spots, a vaguely rhomboid-shaped area, more lightly pigmented than the surrounding area of the shield, was found in all the specimens examined (see Fig. 3.11). This area is most probably TP TSt

**FIG. 3.8: Ventral view of *A. ptyoptera* larval mouth parts. Note the structure and orientation of the maxillary palpus, galea, lacinia and sensillum trichodeum.**

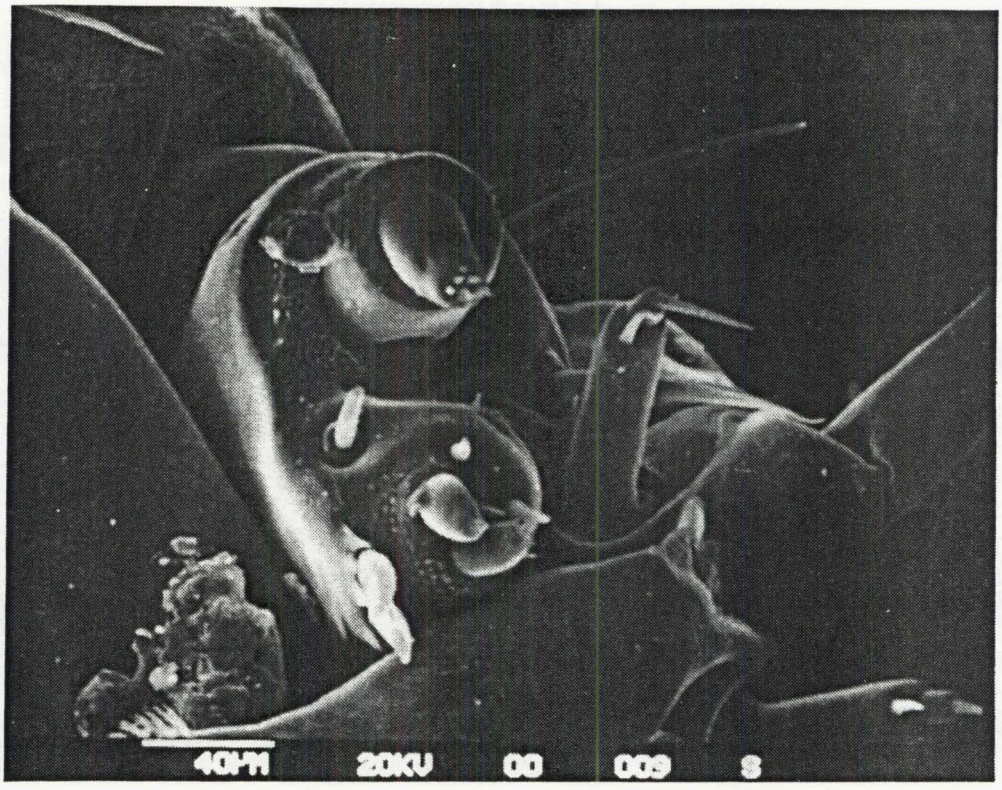



**FIG. 3.9: Spinneret and labial palpi of an *A. ptyoptera* larva**

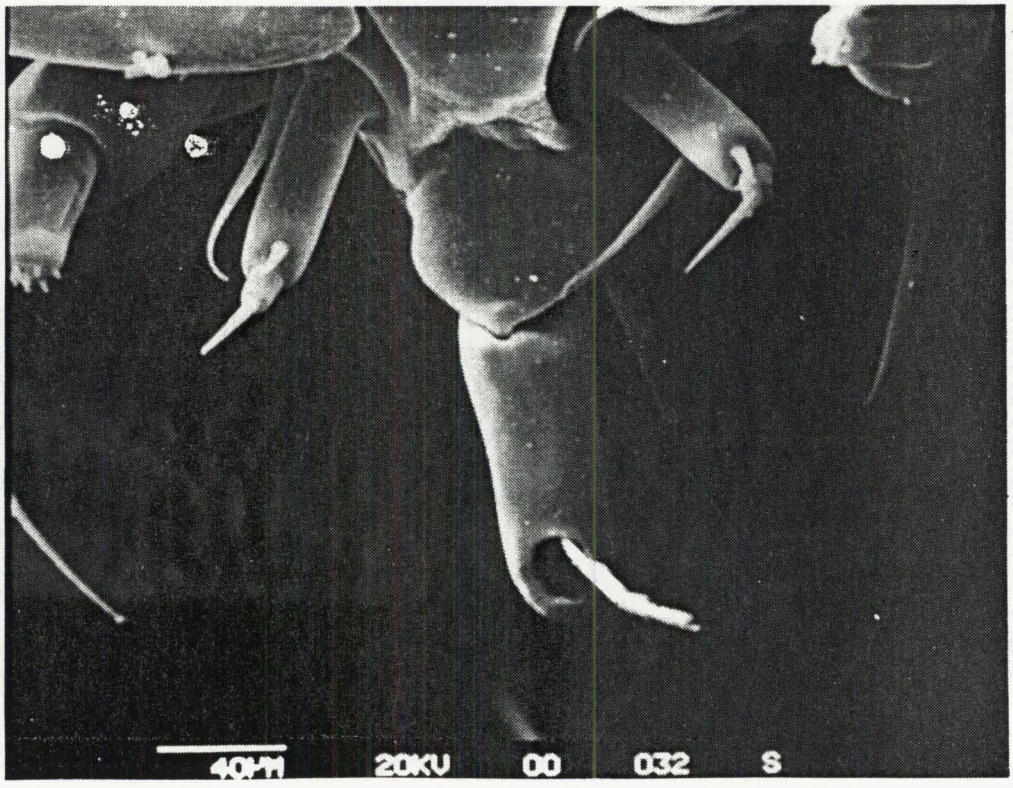


FIG. 3.10: Setal map of *A. ptyoptera* showing the arrangement of setae on the thorax and abdomen of the larvae

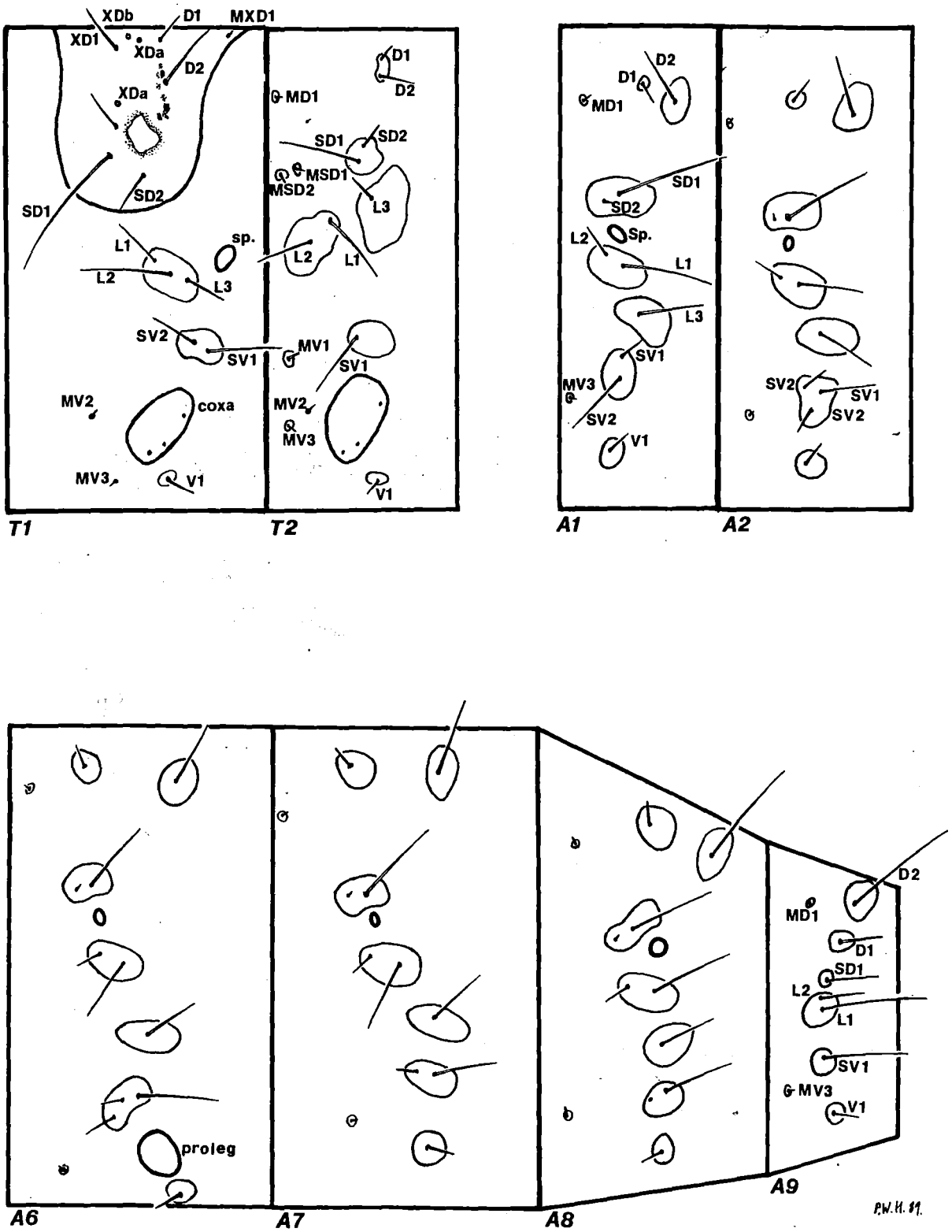


FIG. 3.11: The arrangement of pores and tonofibrillary platelets on the prothoracic shield of *A. ptyoptera* larvae (see text for details)

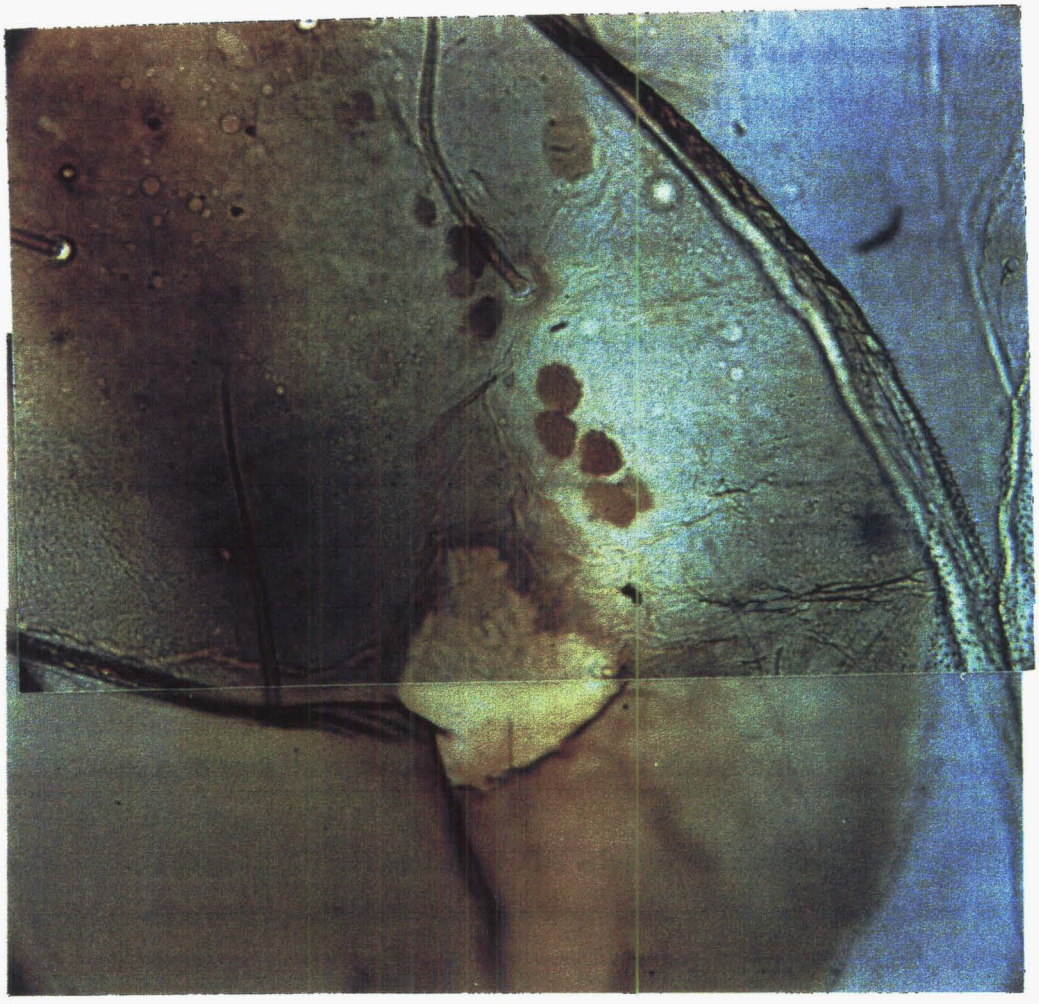
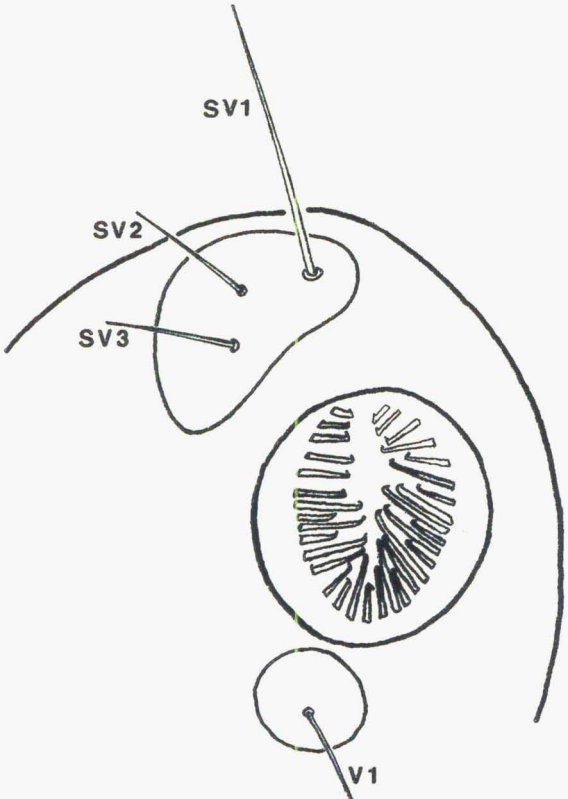


FIG. 3.12: The arrangement of the crochets on the proleg of the sixth abdomenal segment of *A. ptyoptera* larvae



& TP TTr, which are commonly combined (Mutuura 1980). Between specimens, this marking was found to be variable in shape, but consistent in its light pigmentation and placing posterio-ventral to XD2.

The T1 shield pigmented spots of *Anisoplaca arhyrota* (the only other member of the genus examined) differed from the markings of *A. ptyoptera* in that: the TP TSt & TP TTr area is darker than the surrounding shield; TP TIFA 2 is indistinct/ absent; and TP TIC 1, TP TIC 3 and TP TiFA 1 form a large dark area on the dorso-posterior corner of the prothoracic shield. Larvae of some other members of the Gelechiidae (*Aristotelia hermannella*, *Gnorimoshema* sp., *Phthorimaea operculella*) were also examined. Although there were some common features, none of the 50 specimens (4 species) examined displayed a similar tonofibrillary platelet pattern (including head markings) to *A. ptyoptera*.

The arrangement of the pores XDa, XDb and XDc on the T1 shield may also be a useful taxonomic cue (Figures 3.10 & 3.11). Both XDa and XDb are more dorsal than XD1. XDa is situated half way between XD1 and D1. XDb is close to XD1 and is posterio-dorsal to it. XDc is in line with XD1 and SD1 and roughly half way between these two setae.

**ABDOMEN**

D1 of A1-2 is distinctly more lateral than D1 of T2-3. For A1-2 and 6-8, both D1 & D2 are wide of the mid line and D2 is the more lateral. SD2 is close to SD1 on A1-2 and 6-8 and both setae are on one bean-shaped pinacula. SD1 on A1-7 is dorsal to the spiracle and usually at a distance of three times its diameter from it. SD1 on A8 is anterio-dorsal to the spiracle and at a distace of twice its diameter from it. L1 and L2 are on the same pinacula and both are some what ventral to the spiracle, except for A8, where L1 is ventral of the spiracle and L2 is anterio-ventral to it.

The number of setae in the SV group are as follows: on segment A1, two (occasionally one); A2, three (occasionally two); A6, three; A7, two; A8, one (occasionally two); A9, one. This is the typical complement for gelechiids (Stehr 1987).

On segment A9, D1, D2 & SD1 are vertically aligned: D1 is below D2 and equidistant between D2 and SD1. SD1 is quite fine (hair-like). L1 and L2 are close together with L3 absent. SV is unisetose; V1 is present.

Fig. 3.12 shows the organisation and arrangement of the crochets on the A6 ventral proleg (LHS). The arrangement appears to be a uniserial mesal penelipse, with a general pattern (not universal) of alternating biordinal and triordinal sets. The number of crochets varies between 30 and 36. The general crochet arrangement of the A10 ventral proleg is shown in Fig. 3.13a. There were between 12 and 15 crochets arranged in a uniserial, uniordinal transverse row.

**FIG. 3.13a: A ventral view of the arrangement of crochets and setae on the tenth abdomenal segment of *A. ptyoptera* larvae**

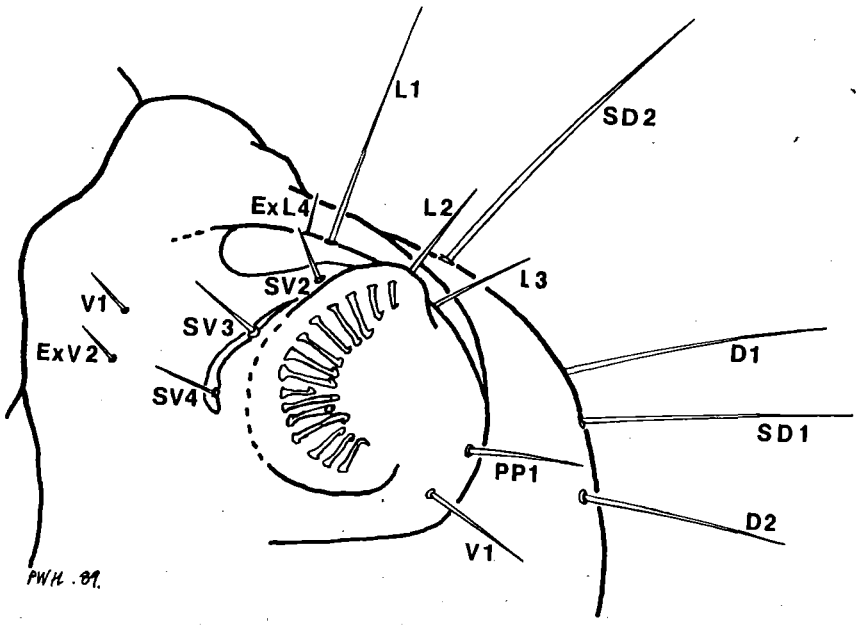
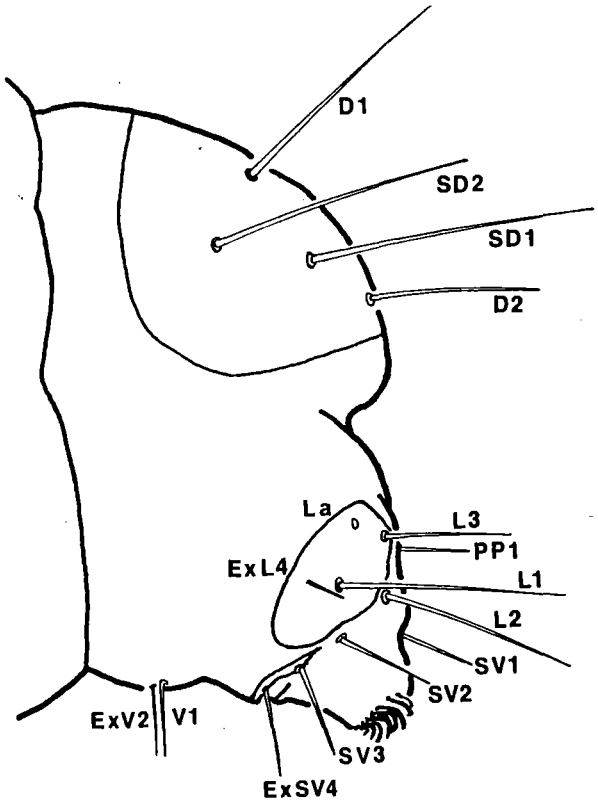



**FIG. 3.13b: Lateral view of the arrangement of setae on the tenth abdomenal segment of *A. ptyoptera* larvae**



Although the A10 chaetotaxy is of limited use at the family level (Hinton 1946, Mutuura 1956), it has proven to be useful at lower levels (Stehr 1987). A10 appears to have a complement of setae standard for gelechiids (as seen in Stehr 1987 p394-399), including the presence and position of EXV2 and EXSV4 (Figures 3.13a & b). However, the arrangement of the A10 setae and some features may be useful diagnostic characters. The A10 setal arrangement is shown in Figures 3.13a & b. Features that may be diagnostic include a thin but distinctly sclerotised and pigmented SV3 & SV4 pinaculum, and a variably present EXL4 (often very small). There is no anal fork.

Tonofibrillary platelets are also present on the anal shield. Although TP TP1 3 and TP TP1 2 markings were present, no regular pattern was found.

## 3.2 Instar Analysis

### 3.2.1 Introduction

Because insects have exoskeletons, postembryonic growth is discontinuous and major increments are limited to periodic moults of the integument. The period between moults is referred to as an instar.

On the assumption that the sclerotised structures of an individual remain constant in size during any given instar, discontinuities in a size frequency distribution have been taken to represent one instar. Head-capsule width or length is the most commonly used measure in such an exercise.

Dyar (1890) is usually credited with being the first to show that the head-capsule widths of successive instars of Lepidoptera formed a regular geometric progression (Gaines & Campbell 1935; Richards 1949). This phenomenon is found in a wide range of insect taxa (Richards & Davies 1977), and was actually described first by Brooks (1886 - cited in Crosby 1973). The Brooks-Dyar rule states that each successive instar is larger by a constant factor, i.e., the inter-instar ratio is constant for each moult.

As part of the larval description, an attempt was made to determine the number of larval instars of *A. ptyoptera*. In this exercise the head-capsule widths of field collected and some laboratory hatched larvae were analysed. The number of larval stages is an important aspect of the insect's biology and is referred to in Section IV.

Daly (1985) gives a through review of the morphometric approaches of instar analysis. Two methods of analysis have been used: i)inspection of a simple frequency distribution of measurements (e.g., Hamon *et al.* 1984); and ii)inspection of a bivariate plot of mean (or modal) instar sizes against the postulated number of instars (i.e., applying the Brooks-Dyar rule) (e.g., Frampton 1984). The use of simple frequency distributions has been critically reviewed by Kishi (1971) and Schmidt *et al.* (1977).

Despite common use, analysis of frequency distributions of morphometric features is often not a reliable indicator of instar number (Kishi 1971; Schmidt *et al.* 1977). In the literature, the source of this unreliability is commonly attributed to two interrelated biological factors:
i) Growth is related to the duration of an instar (i.e., growth proceeds at a constant rate); therefore a regular geometric progression will be found only when the instars are all of the same duration (Richards 1949); and
ii) The instar number often varies, making morphometric analysis difficult or impossible, especially for the later instars. Variation in the instar number can be caused by many things, including: developmental polymorphism (see Schmidt *et al.* 1977), variation in diet (Beck 1950), differences in photoperiod (Honek 1979 - cited in Daly 1985), differences in temperature (Guppy 1969) and starvation (Beck 1972). The number of instars may also vary between the sexes (Vanderwerker & Kulman 1974 - cited in Daly 1985), and the sexes may have different growth rates (Hamon *et al.* 1984).

Therefore frequency histograms 'will give clear results only when the insects being measured are fairly homogeneous in rate of development and number of instars' (Gaines & Campbell 1935).

### 3.2.2 Materials and Methods

The larval populations at two selected sites at Taitapu and Burnham, Canterbury (described in Section 4.2.2.1) were sampled at weekly intervals over the period January 1988 - January 1989. The larvae were extracted from gorse branches, fixed in Carnoy's fluid for 24 hours, then preserved in 70 percent alcohol.

To determine the number of larval instars, the head-capsule width of each larva was measured under a Leitz stereoscopic microscope fitted with an eye-piece graticule. The larvae were measured under 32 times magnification to the nearest 0.0167 mm (i.e., to the nearest graticule unit). Graticule units are used as the unit of measure throughout this study; 1 grat. unit = 1/30 mm. A total of 525 larvae were measured, including 70 laboratory-hatched neonate (first instar) larvae, as these were not extracted efficiently from field samples. The head-capsule widths of the laboratory-hatched larvae and of field collected larvae from both sites are plotted on a frequency histogram. The head-capsule widths of the larvae collected at Burnham are separately plotted in another figure.

### 3.2.3 Results and Discussion

Although frequency distribution analysis works for some species, it is not generally recommended. Most authors favour direct counting of instars, by counting (and sometimes measuring) cast head-capsules, including the one in the pupal cell (i.e., Kishi 1971, Schmidt *et al.* 1977). However, in internal feeders, or other insects whose moults are difficult to determine, the frequency distribution of head-capsule width or length measurements is often resorted to. In this study, frequency distribution analysis was attempted in preference to direct counting because:

i) rearing *A. ptyoptera* from neonate larva was not achieved (see Section 5.3). Although two larvae were reared from early instar to adult, very little emphasis can be placed on the number cast of head capsules because of the scarcity of results. In addition their instar number on collection was not known, and their development in artificial conditions may give an erroneous result.

ii) *A. ptyoptera* often completes development in more than one gallery (see Section 4.3).

iii) *A. ptyoptera* appears to eject cast head-capsules along with frass from the larval gallery. The minute first and second instar head-capsules were rarely found.

If the complex life history of *A. ptyoptera* (see Section 4.2) had been known at the outset of this study, the method used to examine the number of instars would have been seen to be inappropriate. Conversely, the irregular frequency distribution of head capsule widths indicated by this method has been taken as an evidence of a complex life history, including possible developmental polymorphism (i.e., the number of instars is variable) - although this also would have become obvious *via* direct counting.

The head-capsule measurement data are recorded in Appendix II. The pool of all larvae collected and laboratory-hatched larvae is shown in Fig 3.14. Beyond instar I & II, the measurements do not fall into clear groups with modal peaks. Above 22 graticule units, there are many irregular, often abrupt peaks, and their meaning is obscure. However, there are clear troughs in the curve at 12, 16, 27, 39, 52 and 65 graticule units.

Pooling the head-capsule data from more than one source and more than one season may introduce confounding variation (Gaines & Campbell 1935; Richards 1949). To reduce the variation that might have been introduced by pooling, the data from the Burnham site over one season (1988) was plotted separately (Fig. 3.15). Although this frequency distribution obviously suffers from insufficient data points, it appears to follow the same pattern as Fig. 3.14. No clear pattern could be elucidated from this plot either.

Using the larger data set, two mathematical approaches were used in attempts to elucidate a poly-normal trend:
i) a moving average (the average of each value added to the values on either side) was applied to the data. This data transformation failed to clarify the data, and smoothed the existing trends to insignificance; and
ii) a running average ($(x_i+x_{i+1})/2$: $i = 1...n$) was also used to transform the data. This approach emphasised and clarified normal distributions around 20, 54, and 60 graticule units. However, a poly-normal distribution was not produced and the "number of instars" question not clarified.
An "estimation-maximization" (EM) algorithm approach (Beaver & Sanderson 1989) could also have been attempted. However, although this technique may detect a geometric progression, the reality of such a pattern is questionable (Saville pers. comm.). For this vigorous procedure may ignore "real" variation (e.g., that which has a biological cause) and thus may be misleading. The EM approach would be especially inaccurate where developmental polymorphism exists - to use graphical methods, relatively homogeneous populations are needed.

Troughs are unusual in head-capsule frequency distributions because instar ranges usually overlap - especially in the latter instars. Nonetheless, the troughs in Fig. 3.14 may indicate the divisions between the instars. If they do, then there appear to be seven instars. If one assumes this is the case, a rough pattern of bimodalism can be envisaged within the "instar" groups 15-26, 28-39, 40-51 & 53-64 graticule units. Such bimodalism could be the result of: i) different growth rates between the sexes (Hamon *et al.* 1984); or ii) parasitism (Nealis 1987). However, these two possibilities are considered unlikely because: i) although sexing the larvae was not possible, the sexes shared the same size distribution as adults (see Section 4.3.3); and ii) variation in head-capsule widths caused by parasitism would probably be expressed as a group overlapping lesser, non-parasitised instars (See Nealis 1987), not as bimodal distributions.

Another possible explanation of the bimodal trend is where all individuals undergo the same number of instars, but part of the population develop as large individuals and the other half as small ones. The clump of smaller individuals in each "instar" group may become the smaller adults. This possibility is supported by the occurrence of two distinct size classes of adults (See Section 4.3.3, Figures 4.9 & 4.10). However no

FIG. 3.14: Frequency histogram of *A. ptyoptera* larval head-capsule widths. Includes both lab & field collections

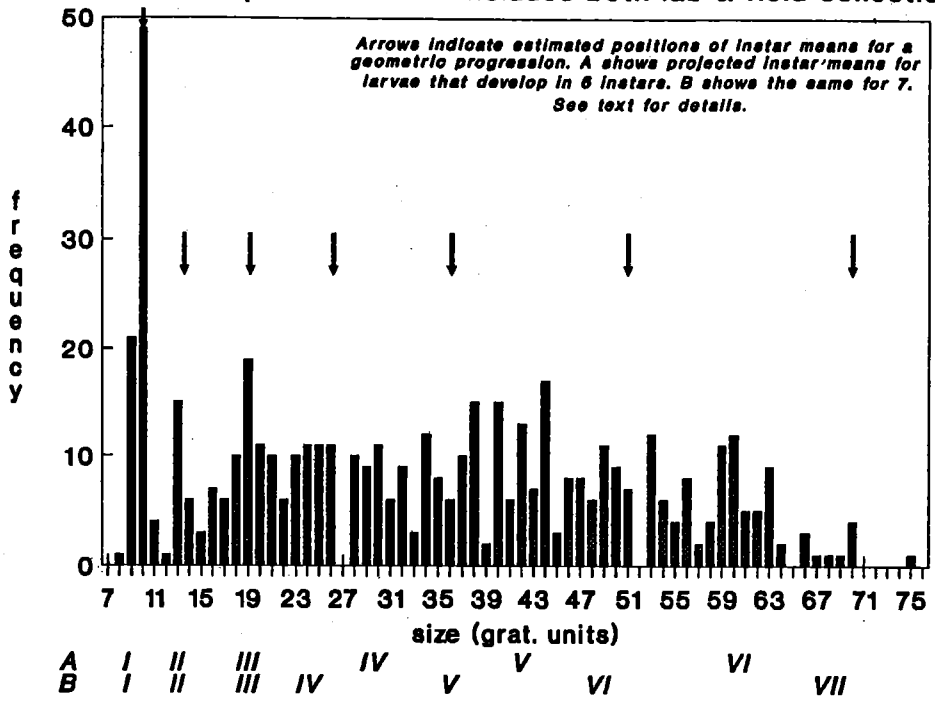
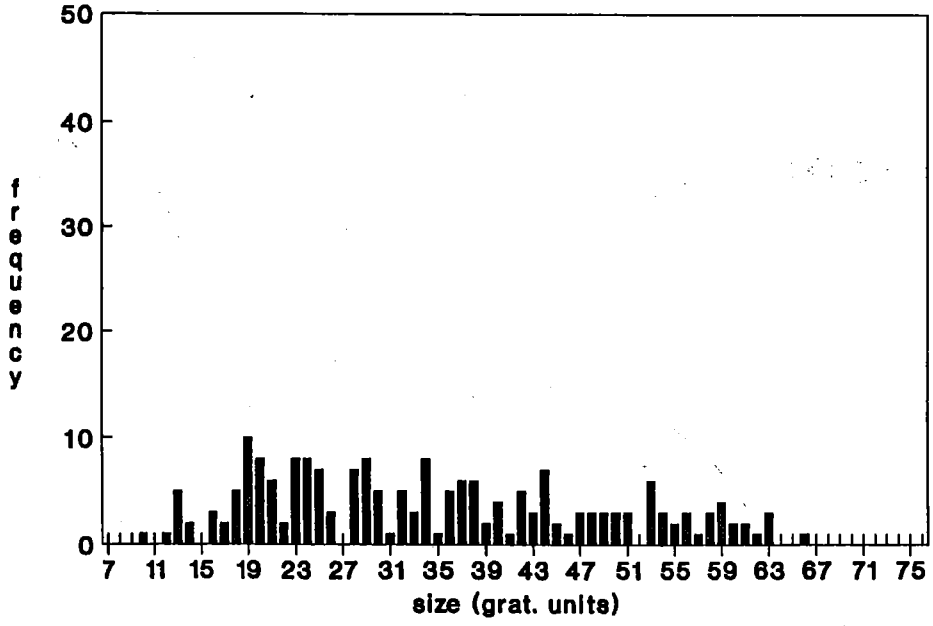



FIG. 3.15: Head-capsule widths of *A. ptyoptera* larvae collected at Burnham MC, 1988.



support for this scenario was found in the literature. In addition the bimodal hypothesis is doubted (for reasons given below). Therefore the preferred explanation for the different adult size classes is variation in the number of instars.

Although the bimodal trend is plausible, the bimodal hypothesis is not considered to be the most likely scenario because: i) I am equivocal about the possible explanations given; and ii) the bimodes do not follow a geometric progression, which, if there were seven bimodal instars, they probably would (i.e., Dyar's law).

The geometric progression which normal development would be expected to follow can be estimated by:
i) calculating the mean values of the relatively clearly distinguishable instars I & II (the values used in this calculation are shown in Appendix Table II.2); and
ii) generating Dyar's constant from the calculated means of instars I & II. Then;
iii) assuming the Brooks-Dyar Law to be true, the calculated Dyar's constant can be applied to generate estimated instar means for a geometric progression, i.e.,
Dyar's constant (Y) = mean of instar one ($\bar{x}_1$)/ mean of instar two ($\bar{x}_2$)
i.e., $Y = \bar{x}_1 / \bar{x}_2$
@ $\bar{x}_2 = \bar{x}_1 / Y$
The calculated and estimated mean values are shown in Table 3.1 and indicated on Fig. 3.14 as arrows. Other Dyar's ratio progressions were calculated using different frequency values and a calculated mean for instar III. However these "alternative means" required greater estimation (in the tail of the groups), therefore the progression shown is thought to be the most representative.

**TABLE 3.1: Calculated and estimated (*) mean head-capsule widths of *A. ptyoptera* (in graticule units), assuming a geometric progression.**

| INSTAR | MEAN HEAD-CAPSULE WIDTHS (GRATICLE UNITS) | INTER-INSTAR RATIO (DYAR'S CONSTANT) |
|---|---|---|
| I | 9.75 | 0.7199 |
| II | 13.54 | |
| III | 18.81* | |
| IV | 26.12* | |
| V | 36.28* | |
| VI | 50.4* | |
| VII | 70.01* | |

Apart from a good fit on the clear peak at 19 graticule units, no obvious trend follows the estimated geometric progression. The lack of a single geometric pattern in the data can be taken to indicate developmental polymorphism. In this scenario, the number of instars is not fixed: some individuals may undergo perhaps five instars, some six and others more. If this is taken to be the case, and the larvae reach roughly the same end point, then the duration and increment in size between the instars will be different for

each development morph. Such developmental polymorphism would produce a complex frequency distribution from instar III or IV onwards, such as we see in Fig. 3.14 (cf. Schmidt *et al.* 1977).

Developmental polymorphism is considered the most likely possibility in *A. ptyoptera* because of a combination of:
i) the complex head-capsule width frequency distribution with many obscure peaks which do not conform to a geometric progression (cf. Gains & Campbell 1935); and
ii) *A. ptyoptera* has a loose seasonal life history with a long period of oviposition and a non-synchronised larval development (see Section 4.2). Such a complex life history may, in part, be maintained by variable larval development strategies. Development polymorphism is likely to be both genetically and environmental determined, and maintained by shifting selection pressures.

A model of developmental polymorphism fits the frequency distribution of *A. ptyoptera*, which lends further support to the developmental polymorphism hypothesis. If one assumes most of the larvae undergo either of two development paths, one of six instars and the other seven, then the development patterns of other Lepidoptera with two development paths (e.g., Gaines & Campbell 1935, Morris & Fulton 1970, Schmidt *et al.* 1977) can be used to assign possible meanings to the peaks in the frequency distribution of *A. ptyoptera.*

The postulated model is fitted along the bottom of Fig. 3.14 with the "A" series being estimated mean head-capsule widths for larvae completing development in six instars, and "B" the same for seven instars. The model does not fit the frequency distribution perfectly, as the peak at 53-56 graticule units does not fall within the scheme. However, this deviation may be the consequence of parasitism, which is high in *A. ptyoptera* populations (see Section 4.4). Variation caused by parasitism or other influences would become most apparent in the latter instars. So if the polymorphism model is taken as a satisfactory estimation of the data, it is projected that most larvae complete development in either six or seven instars.

It is likely that the number of instars an individual undergoes influences its size as an adult. There are two alternative possibilities:
i) the individuals that have a development path of the fewest instars become the smallest adults - and the largest adults have the most instars. This hypothesis may be supported by there being fewer individuals in both the larger size class of adult (33 percent large) and in the largest group of larvae (66 - 70 grat. units), with 16 percent in the large group. (The smaller group is taken to be 58 - 64 grat. units). Although, the difference between the two groups of larvae may be due, in part, to parasite induced mortality.
Alternatively;
ii) the different development paths may all achieve similar sized adults. In this case, the smallest adults may arise from individuals that shorten their length of development by one (or more) instars because of unfavourable conditions or some other untoward situation.

### 3.2.4 Sub-Section Summary

The number of larval instars of *A. ptyoptera* is not known. The frequency histogram of head-capsule widths does not follow a geometric progression. Therefore it is proposed that *A. ptyoptera* has a complex development pattern - this is almost certainly part of a complex life history. This study supports the argument that head-capsule widths are not reliable for determining and, *via* Dyar's rule, corroborating the number of larval instars.

A number of alternative models can be proposed to explain the observed pattern. The possibility considered most likely is a developmental polymorphism where most of the larvae develop in either six or seven instars. An associated possibility is discussed where the size of the resultant adult is a consequence of the number of instars undertaken. It should be noted that any pattern within the frequency distribution is likely to be distorted by variation caused by parasitism, variation in food quality etc.

Although the number of instars could not be determined precisely, the instar analysis has not been a futile exercise. The resultant head-capsule frequency histogram of *A. ptyoptera* is taken as an indication of a complex life strategy. Further the seasonal progression of head-capsule widths gives valuable focus to the study of seasonal distribution of life stages (Section 4.2).

# *SECTION IV: The Biology of A. ptyoptera*

## 4.1 Section Introduction

Compared to countries with an extensive and long history of biological research, both the biology and taxonomy of the New Zealand insect fauna are under-studied and hence, in general, poorly understood. This is true for *A. ptyoptera;* before this study, all that was known about the insect was some limited data on its distribution, its host range and its damage to gorse. Very little of this information had been collated and published.

Some New Zealand insects that attack exotic pesty animals and plants offer potential as biocontrol agents within or outside New Zealand (Hill unpub.), but in most cases the biology of these insects is insufficiently understood to allow their exploitation. Of the New Zealand insects that attack exotic weeds, *A. ptyoptera* seems to be the only one that has been considered as a candidate biocontrol agent.

Such consideration runs contrary to the conventional practice of searching for candidate agents in the weed's region of origin and/or evolutionary centre (see Section 2.4.4.1). However the potential biocontrol use of *A. ptyoptera* is in agreement with Hokkanen & Pimentel (1984, 1989) who proposed new associations (including those in novel geographic regions) offer better potential for biocontrol success. Hokkanen & Pimentel's proposial has been disputed by Goeden & Kok (1986), Harris (1986), Lawton (in press) and others (see Section 5.1). Nevertheless some new associations can and do provide good control (Denhill & Moran 1989; Hokkanen & Pimentel 1989) and this approach is worth consideration, albeit with some trepidation concerning host specificity.

This study represents the basic research on *A. ptyoptera* needed before commencing thorough host specificity testing. In this section the following aspects of the biology of *A. ptyoptera* are investigated: the seasonal distribution of life stages; larval feeding sites; the incidence of parasitism; and fecundity and fertility. Although these aspects (and the instar determination) are reported individually, they are, as will become apparent, intimately linked to each other and should all be viewed in combination.

## 4.2 Seasonal Distribution of Life Stages

### 4.2.1 Introduction

Since insects are organisms whose state largely varies with that of their surrounding medium (e.g., poikilothermic), the rate at which they grow, develop, reproduce and die, and the way in which they behave is determined by the prevailing biotic and abiotic environment. The adaptations that species have developed to track annual spatio-temporal fluctuations in habitat favourability are known collectively as seasonal responses. Such responses include dormancy, seasonal migration and seasonal polyphenism, or any combination of the three (Tauber *et al.* 1986), along with the insects' general phenology.

Studies of seasonality consist of three parts: i) field studies of the normal timing of life history events (especially periods of inactivity) and the identification of any possible limiting environmental factors; ii) laboratory studies of factors affecting periods of dormancy and activity; and iii) interpretation. This study has concentrated on the first part of this series.

### 4.2.2 Materials and Methods

#### 4.2.2.1 Study Areas

The material used in the examination of the seasonal distribution of life stages (4.2), larval behaviour (4.3), incidence of parasitism (4.4) and instar determination (3.2) was all derived from the same sampling programme.

It was envisaged that the use of two climatically contrasting sites would allow the comparison of different biological regimes. Two sites in Canterbury were chosen: one at the Selwyn Plantation Board forest at Burnham, and the other on a southerly slope on the Port Hills, behind Taitapu. The study areas will be referred to as Burnham and Taitapu respectively.

**Burnham**

The Burnham site was situated in the Selwyn Plantation Board planting at Burnham MC (map reference: M36 555318). The site was defined as a 500 by 200 m strip. The trial plants consisted of a moderate to dense infestation of gorse (0.167 - 4 stems/m) growing between the rows of *Pinus radiata* (see Fig. 4.1). At the commencement of the study (in August 1987) the pine plantation was 5 years old and the gorse plants ranged from seedlings to plants four years old. The gorse stand here had been undisturbed by control attempts for four years. Most of the plants were then three years old (it should be noted that age determination of gorse plants is not "fail safe"). Apart from some rabbit grazing, the Burnham gorse was under no apparent vertebrate herbivore pressure.

**FIG. 4.1: The Burnham field site, November 1987. Situated in the Selwyn Plantation Board *Pinus radiata* plantation at Burnham, Canterbury.**

**FIG. 4.2: The Taitapu field site, November 1987. Situated on the property of Mr & Mrs Sullivan, Taitapu, Canterbury.**

The Burnham site was characterised by a high degree of shelter from the wind due to the pine trees (approximately three metres tall), but as the pines were only 5 years old, the degree of shading was low. The gorse plants were healthy and the population vigorous.

**Taitapu**

The Taitapu site was situated on the property of Mr & Mrs Sullivan (Trafalgar Farm - map reference: M36 781268). This site was chosen to contrast with the sunny, sheltered site at Burnham. As opposed to the plain setting of Burnham, the Taitapu site was a 500 by 200 m strip situated down a variably sloping incline. The site was south-facing. The elevation of the site ranged from 340 m to 200 m (Fig. 4.2).

The site vegetation was predominantly pasture with scattered bushes and clumps of gorse. At the commencement of the study the gorse plants at Taitapu ranged from two to roughly six years old. The average age was 3.5 years old.

The Taitapu plants were subject to sheep and some limited goat grazing. As a result, the plants exhibited a much more dense growth pattern than Burnham. The high degree of wind exposure may also have contributed to the observed growth form.

#### 4.2.2.2 Methods

August - December 1987 was a period of preliminary investigation. This brief survey afforded an evaluation of the moth's biology, and the information gathered in this period allowed the development of a sampling plan as well as providing the knowledge base for the laboratory studies undertaken over the summer of 1987-88 (fecundity trials (Section 4.6), culturability (5.3), damage assessment (5.2)).

Four approaches were adopted in determining the seasonality of *A. ptyoptera*. The first was the collection and review of all the available information on *A. ptyoptera*. In addition to the literature mentioned in 2.2, this included gaining access to the National Arthropod Collection, DSIR Plant Protection (Auckland), as well as the insect collections of the Auckland War Memorial Museum and institute; Ministry of Agriculture and Fisheries (Lynfield, Auckland); National Museum of New Zealand (Wellington); Forest Research Institute (Rotorua); Lincoln University; and the private collection of Mr Brian Patrick (Dunedin). Information was also gathered from the files of MAF Quality Management, Plant Protection Centre (Lincoln).

The second approach was to monitor the life history events at the two field sites in Canterbury and attempt to relate these events to the prevailing season. From January 1988 to March 1989 the life stages and parasite particulars of *A. ptyoptera* at the Burnham and Taitapu sites was monitored weekly. The sample unit was a randomly selected infested gorse branch from each site. The growth pattern of gorse has been described in Section 2.3.5. For the purposes of this study, a modification of Cassie (1954) was adopted for

referring to the various wood age goups of gorse folige. The current season's growth is referred to as G0, the preceding year's growth G1, and so on. A "branch" is defined as the part of a gorse bush from G4 inclusive (or the bush's origin if under 4 seasons old), one G3 derivative and all the succeeding G2, G1 and G0 derivatives.

The selected branches were taken back to the laboratory and their surfaces searched for eggs. The spines were then removed from the branches by running a knife down the surface of the branch, taking care not to damage the bark. The branches were then dissected by carefully removing the bark strip-wise. The presence of galleries and *A. ptyoptera* life stages or parasites therein was noted. The branches were then split lengthwise in case any larvae boring in the pith had been over-looked.

The location of the rarely found eggs was noted and the eggs kept at room temperature to monitor emergence and incidence of egg parasites (see Section 4.4). After noting their position within the branch (used in assessing larval behaviour (Section 4.3)), the larvae obtained were fixed in Carnoy's fluid (see Appendix I) for 24 hours then preserved in 70 percent alcohol. Additional larva were obtained by periodic intensive searching and dissection at the study sites over the same period. The larvae were subsequently used in the instar determination (Section 3.2). Live pupae were kept in the small section of branch in which they occurred, with the covering bark tied back over them. These were then kept at ambient room temperature (roughly 14-27°C; mean 22°C) and the timing of their emergence recorded. The position and estimated age of emerged pupal cases was also noted.

It was envisaged that the determination of the meteorological characters of the two sites would enable the occurrence of life history events and other biological aspects to be related to the prevailing environment. Because the meteorological information available from Burnham Military camp and Lincoln (the nearest weather stations) would be widely different from that experienced at the experimental sites, the site temperatures, precipitation and wind run over the period Jan 88 - March 89 were recorded at each site. The temperature and humidity were recorded on a Casella (clockwork rotating drum) Thermo-hygrograph. This was housed in a Stevenson screen that was 100 mm above the earths surface. Wind run (kms) was measured on a Lambrecht anemometer. This was set on 1 m high tripod that was guyed down. Precipitation was measured in a 125 mm diameter rain gauge.

The third approach used to assess the seasonal distribution of life stages was to culture larvae on general purpose artificial diet (GPD) (Singh 1983). It was envisaged that laboratory rearing would allow the manipulation of the moth's biology (at different temperature and photoperiod regimes) and hence allow determination of the type of over-wintering strategy (quiescence or diapause) as well as the assessment of development rate - temperature relationships (i.e., development thresholds, physiological time). For this assessment larvae were collected from infested gorse branches from Springston and Greenpark, Canterbury, during October and November 1987 and brought into the laboratory. Twenty mid-range instar larvae were introduced to GPD in lugless plastic petri dishes. Half of this culture was placed in a controlled temperature cabinet at 18°C and LD 10:14 the other half was placed in a separate cabinet at 18°C LD 16:8.

In August 1988 eight instar II - III, 19 instar IV - V and 14 instar VI + larvae were introduced to GPD in 10 x 80 mm plastic test tubes. This culture was maintained at room temperature.

As it became apparent that *A. ptyoptera* does not have a straight-forward life history, a further approach was used in an attempt to bring the issue of voltinism into sharper resolution. The fourth approach to investigating the seasonality was to use the seasonal progression of instars as estimated by head-capsule measurement. The results were analysed graphically using two techniques:
i) by plotting the monthly head-capsule width range and mean against time as a line graph; and
ii) the construction of frequency histograms of the head-capsule measurements divided into bimonthly groups.

### 4.2.3 Results and Discussion

The results of the investigation into the seasonal distribution of life stages are recorded in Appendix III. Appendix Table III.1 contains the information from the collection review and weekly field monitoring approaches. The results of the 1988/89 GPD trial are shown in Appendix Table III.2. The results from Appendix Table III.1 are diagrammatically summarized in Fig 4.4, 4.5, 4.6, & Table 4.1. The meteorological data from the two sites over the study period are shown in Figures 4.3a, b & c. The information from the monthly examination of head capsule properties is expressed in Fig. 4.7, and the bi-monthly comparison in Fig. 4.8.

**Seasonal distribution of life stages**

The most notable aspect of the seasonal life history of *A. ptyoptera* is that each event occurs over a long period and appears to be little synchronisation of events. This appears to arise from the low degree of synchronisation between individual members of the population. This lack of synchrony is evident both nationally and locally.

My original intention was to use the meteorological characters of the Taitapu & Burnham sites to relate the occurrence of life history events and other biological aspects to the prevailing environment. However, a comparison of the sites was not undertaken because i) as shown by Figures 4.3a, b & c, with the exception of wind run, the climate experienced at the two sites was not dramatically different; and ii) the life events at both sites were similar in their timing and low degree of synchrony. In addition, because of the difference in the history and management of the two sites, such a comparison may not have been viable anyway. Further, quantifying insect development by meteorological data to is probably not realistic given that meteorological information is notoriously different from that experienced in the creature's micro-habitat (e.g., Pinter *et al.* 1975).

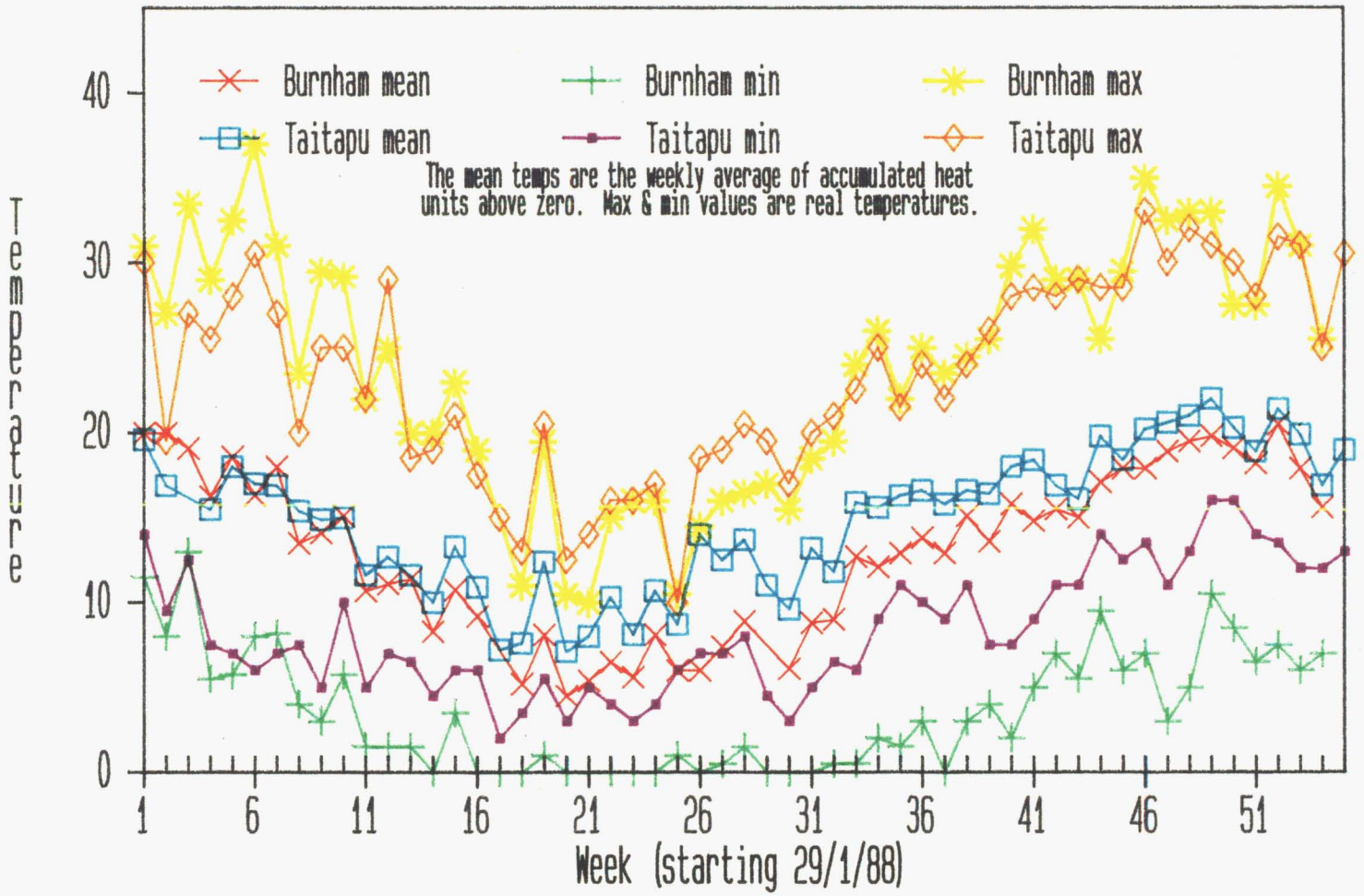

Burnham mean
Burnham min
Burnham max
Taitapu mean
Taitapu min
Taitapu max
The mean temps are the weekly average of accumulated heat units above zero. Max & min values are real temperatures.
Temperature
0
10
20
30
40
1
6
11
16
21
26
31
36
41
46
51
Week (starting 29/1/88)

FIG. 4.3b: Rainfall (mm) at the Burnham & Taitapu field sites over the study period

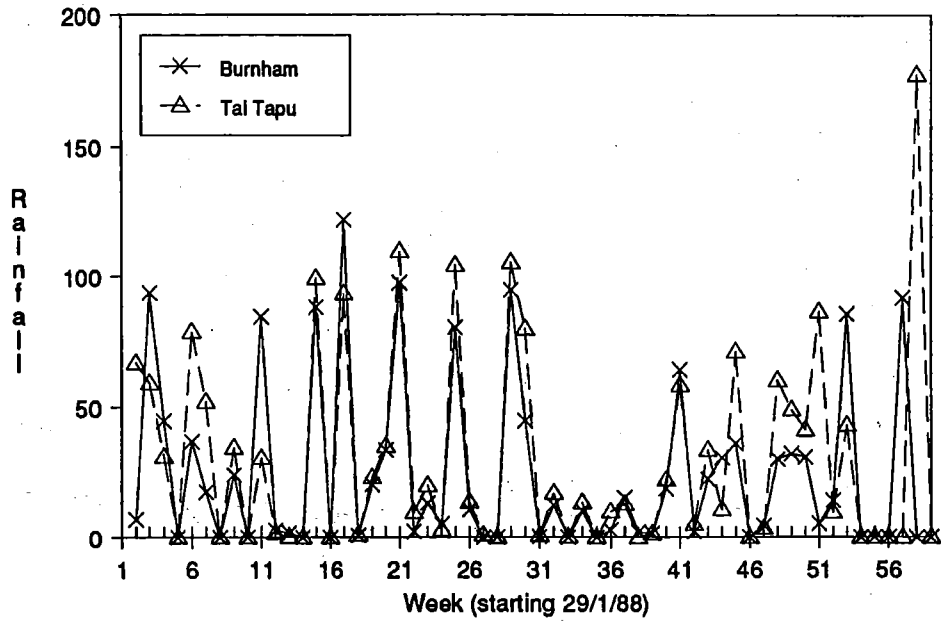
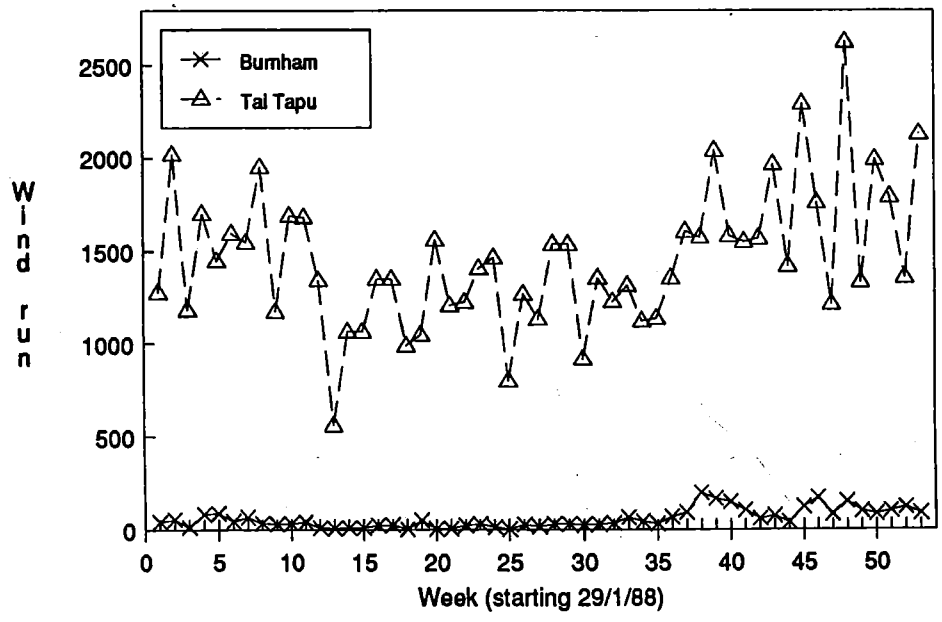



FIG. 4.3c: Wind run (km) at the Burnham & Taitapu field sites over the study period



**i) Adults:** Of the four approaches adopted to examine seasonality, the literature and collection search gave an insight into times of adult flight activity as well as some information on the distribution of the moth (Section 5.5), recorded host plants (Section 5.4) and the existence of parasites (Section 4.4).

Hudson (1928) and Butler (1979) suggested that adults emerge in January and February. The adult collection data (from Appendix Table III.1) is summarised in Figures 4.4 & 4.5. Although these data span the years 1917-1988 and are from throughout New Zealand, they indicate two things; i) nationally, adults occur from Oct to May; and ii) there appears to be one period of emergence.

**TABLE 4.1: First and last observations of adult *A. ptyoptera***

| | First observation | Last observation |
|---|---|---|
| **Collection review** | 24/10/1924 ChCh. MC | 6/5/1962 Reefton Saddle,BR |
| **This study** | 1/11/1988 Lincoln, MC | 7/3/1989 Lincoln, MC |

This study monitored the occurrence of adults from gorse sticks brought into the laboratory. Although artificial conditions were imposed on the specimens, the behaviour from one place over one season can be examined. The adult emergence data from Glenroy, MC, over the 1989-90 season are shown in Fig. 4.5.

Figures 4.4 & 4.5 indicate *A. ptyoptera* adults occur mainly in December, January and February. In Glenroy, MC, the peak emergence in 1990 covered January and February, but in warmer parts of Canterbury (e.g., Burnham & Taitapu) the peak appears to occur mainly in January.

The low degree of synchrony in the life history events of *A. ptyoptera*, as referred to above, is expressed in the overlap in the timing of the events (see Fig. 4.6) and also in the prolonged period of adult emergence (see Table 4.1) - the period between the first observed adult and the last is six and a half months, although the span observed within one season was 4 months. This contrast reflects the limited data collected within one season (see Wolda 1979; 1988).

The long period of adult flight activity, coupled with a longevity of four to seven weeks for females, results in a prolonged period of oviposition. Such a lengthy period of oviposition would presumably maintain the low degree of life history synchrony observed. Indeed, there is a corresponding broad spread in instars at any one time (see range bars of Fig. 4.7), although variable environmental factors would also contribute to variation in larval development.

FIG. 4.4: The occurrence of *A. ptyoptera* adults each month in New Zealand. SOURCE: collection records, 1917-88

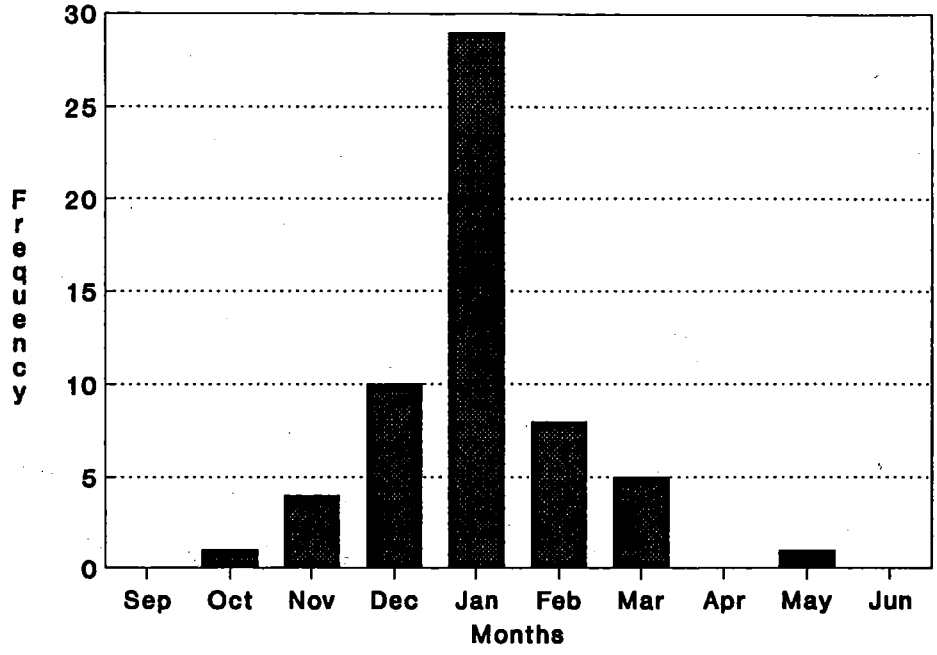



FIG. 4.5: The emergence of *A. ptyoptera* adults from Glenroy, MC. 1989-90

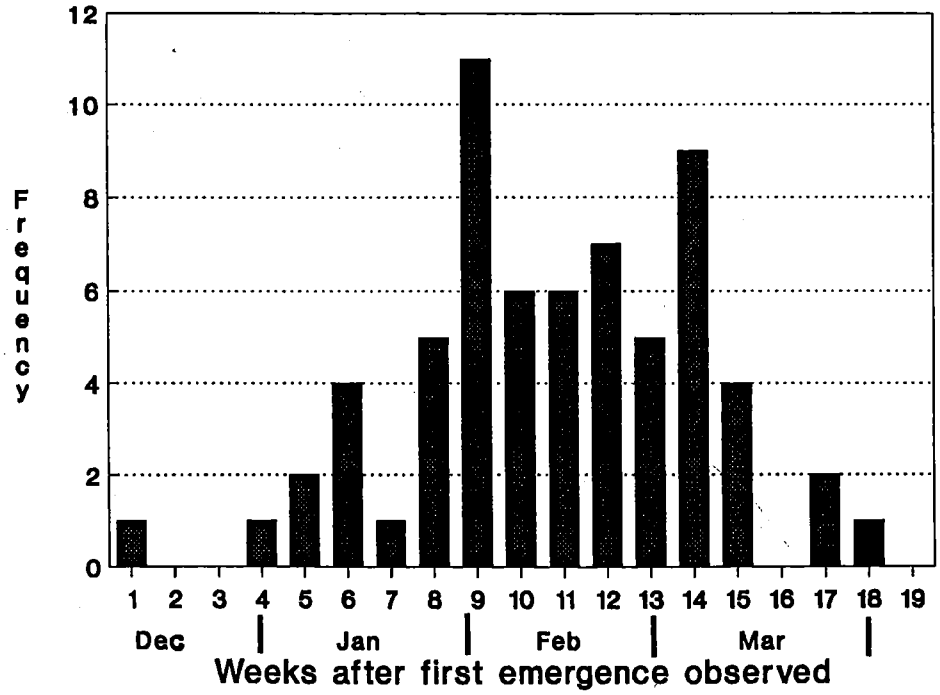


FIG. 4.6: Seasonal life history of *A. ptyoptera* in Canterbury

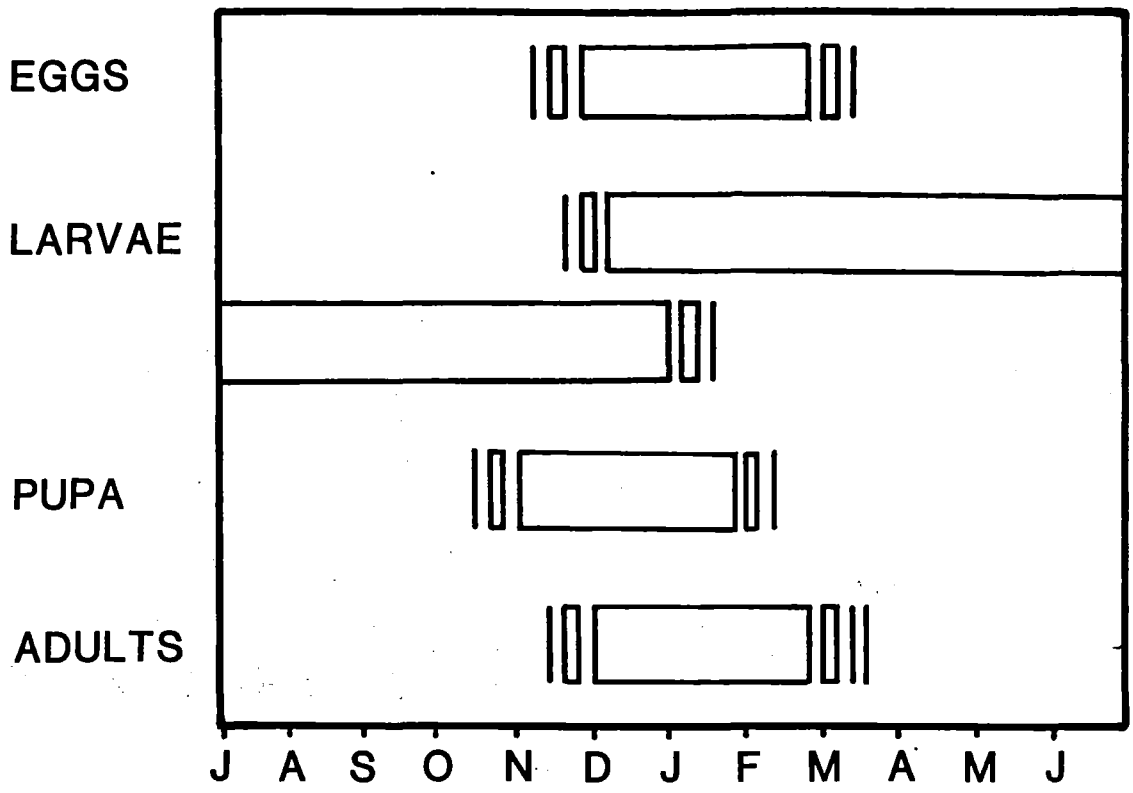
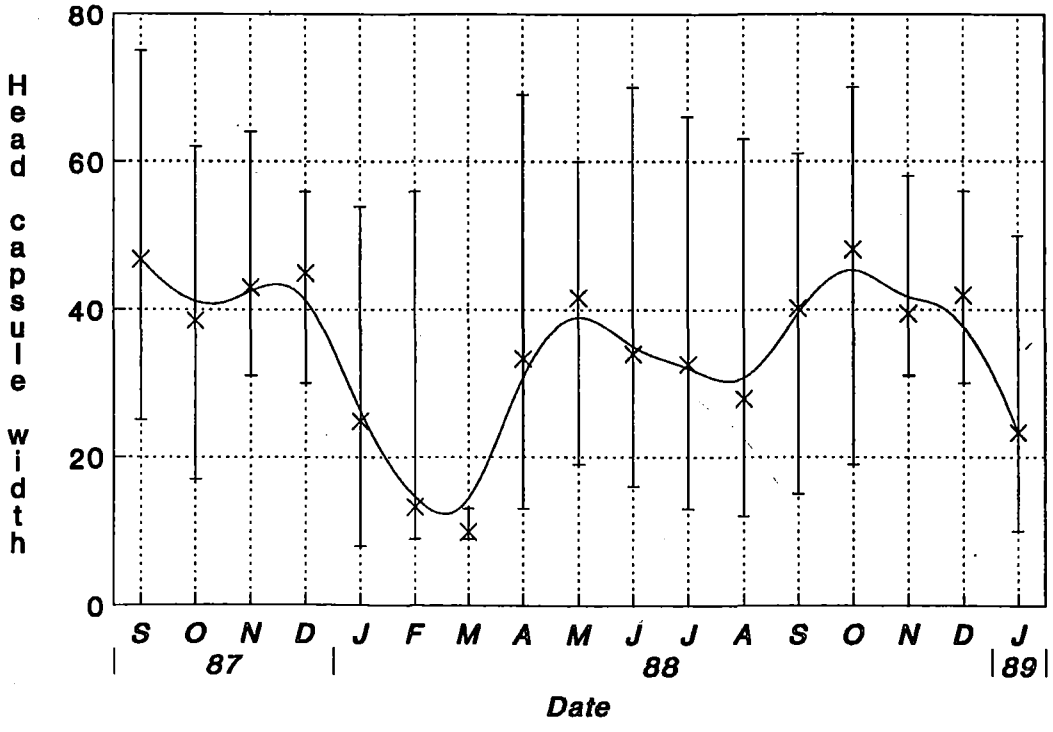



FIG. 4.7: Monthly mean head-capsule widths of *A. ptyoptera* larvae
Units = graticule units, bars indicate range.



**ii) Immatures:** The seasonal distribution of the immature life history stages was ascertained from the field monitoring exercise (second approach). The results from this exercise are recorded in Appendix Table III.1 and expressed in Figures 4.6 & 4.7.

Eggs were found in the field on only four occasions. These were all between 12th Jan & 24th Feb. However, oviposition was observed in the laboratory over the period 28th Dec - 3rd March, so it is assumed that egg laying occurs over nearly the entire period of adult occurrence. Yet oviposition is unlikely to be at a constant rate over this period, because low humidity and cold (not measured) both appear to limit oviposition (Hill *et al.* unpub.).

Larvae occur at all times of the year (Fig. 4.6). At any one time there is a broad range of instars present (Fig 4.7), although neonate larvae were found only in the Jan-Feb period. Most instars appear to be represented in the summer, autumn and winter months, but in November and December there is a tendency to the later instars (Fig 4.8). As larval development is not synchronised, the period over which *A. ptyoptera* damages its host spans the entire reproductive and growth phenology of gorse (see Fig. 2.1).

The earliest pupa was recovered in early November. However, given that adults were also recovered in early November and pupal development takes 2 to 4 weeks, pupation probably begins in October. Pupal numbers were found to peak in December, then decline and finish through February.

**Voltinism**

A key issue in this section of the study was determining the voltinism of *A. ptyoptera*. This issue includes two questions: i) what is the voltinism? and ii) is a consistent pattern expressed? As *A. ptyoptera*, apparently like many other New Zealand insects (Dugdale pers. comm.), has a "diffuse" or "plastic" life history, this study was unable to determine the voltinism with absolute certainty. Yet the bulk of the evidence and data which are outlined below suggest that the moth is univoltine.

Although the occurrence of adults spans from October (spring) to May (late autumn) (see Table 4.1), there appears to be a single peak of emergence in December and January (Figures 4.4 & 4.5). This suggests just one period of emergence, albeit an extended one . In addition, the progression of life history events (as shown in Fig. 4.6), although not synchronised, appears to follow an annual trend.

An alternative interpretation is that the prolonged adult emergence and broad spread in larval sizes are due to part of the population having a bivoltine life cycle. This possibility is supported by some of the laboratory culture progressing from early instar to pupa within 3 to 4 months (see Appendix Table III.2). However, there is no way of knowing the absolute age of these larvae, the conditions they had been exposed to before capture or what their performance may have been under natural circumstances.

Because the data from the first three approaches were not conclusive, the progression of larval instars was examined. Fig. 4.7 shows the monthly average and range in head capsule measurements. Although the curve in this figure is not a smooth annual sine wave typical of a univoltine insect, there is a trough over the Jan, Feb, March period and a tendency to peak in spring. These trends are weak, however, and the data are unlikely to be representative because of the inclusion of many laboratory hatched larvae during Jan, Feb and March. Thus this graphical examination is of limited applicability here and the more thorough Fig. 4.8 used.

Fig. 4.8i, and to a lesser extent 4.8iii, suffer from skewedness caused by inclusion of laboratory data. Figure 4.8ii & 4.8iv are solely field data covering the same period, but because instars I and II are difficult to find in the field, these graphs are also unlikely to be an accurate representation of the real situation. Therefore the interpretation of graphs 4.2ii & iv should be weighted taking into account the under representation of early instars (and possibly of VI & VII too, due to attrition by parasitism).

Although this aspect of the study may suffer from insufficient data points (despite through searching), the progression of Fig. 4.8i to viii follows a perceptible trend. This trend is as follows:
i) Many early instar larvae in Jan-Feb as well as several, perhaps imminently pupal, later instar larvae.
ii) In March-April, the latter instars are less well represented, presumably because most of the larger larvae have emerged. In this period there is a tendency to instar III.
iii) The winter months (May-Aug) still predominantly earlier instar larvae, but there is a greater proportion of instars IV & V than in Jan-April, indicating that the population is maturing.
iv) The period Sept-Oct shows a increase in head-capsule widths, with a tendency to IV,V & VI.
v) In Nov-Dec the trend of increasing widths is especially strong with a distinct grouping around instar V and very few early instar larvae. These few small larvae in this period may, in fact, be the offspring of the current season's early emerging adults.

It is the trend outlined in the above paragraph, combined with the trend shown in Fig. 4.6, that leads me to suggest *A. ptyoptera* is univoltine, although its life history events do not appear to be synchronised and show considerable overlap. It is quite possible that univoltinism is not obligatory; a few individuals that are laid early in the season and develop in favourable conditions may complete their life cycle in 5 or 6 months and emerge in late summer. Also the occurrence of late instar larvae over the winter months (Figures 4.8v & vi) may be an indication that some individuals undergo a second winter. This may be a result of being laid late in the season and/or encountering sub-optimal conditions. Such occasional semivoltinism was found in typically univoltine currant clearwing populations by Brock *et al.* (1964) and Scott (1975). This is believed to be the result of feeding in older, less nutritive wood, and possibly some low temperature effects (Scott pers. comm.)

Another possibility is that some individuals undergo fewer instars, perhaps by deliberately foregoing a later instar, and emerge as smaller adults (for discussion see Section 3.2.3). Such an ability would afford considerable life history flexibility. This possibility is supported by the finding of two distinct size classes.

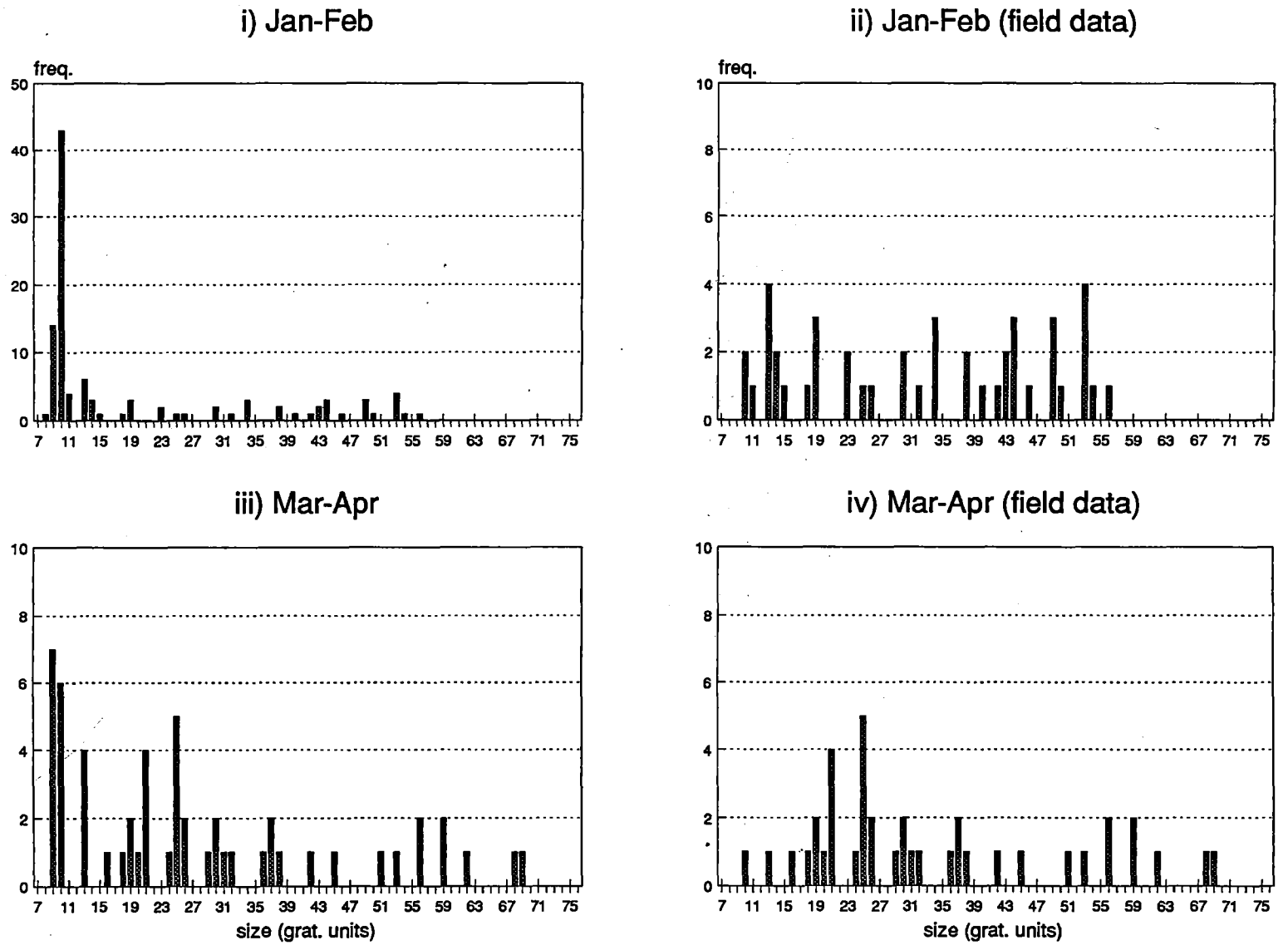



FIG. 4.8: *A. ptyoptera* larval head-capsule measurements divided into two monthly intervals.

FIG. 4.8 Continued

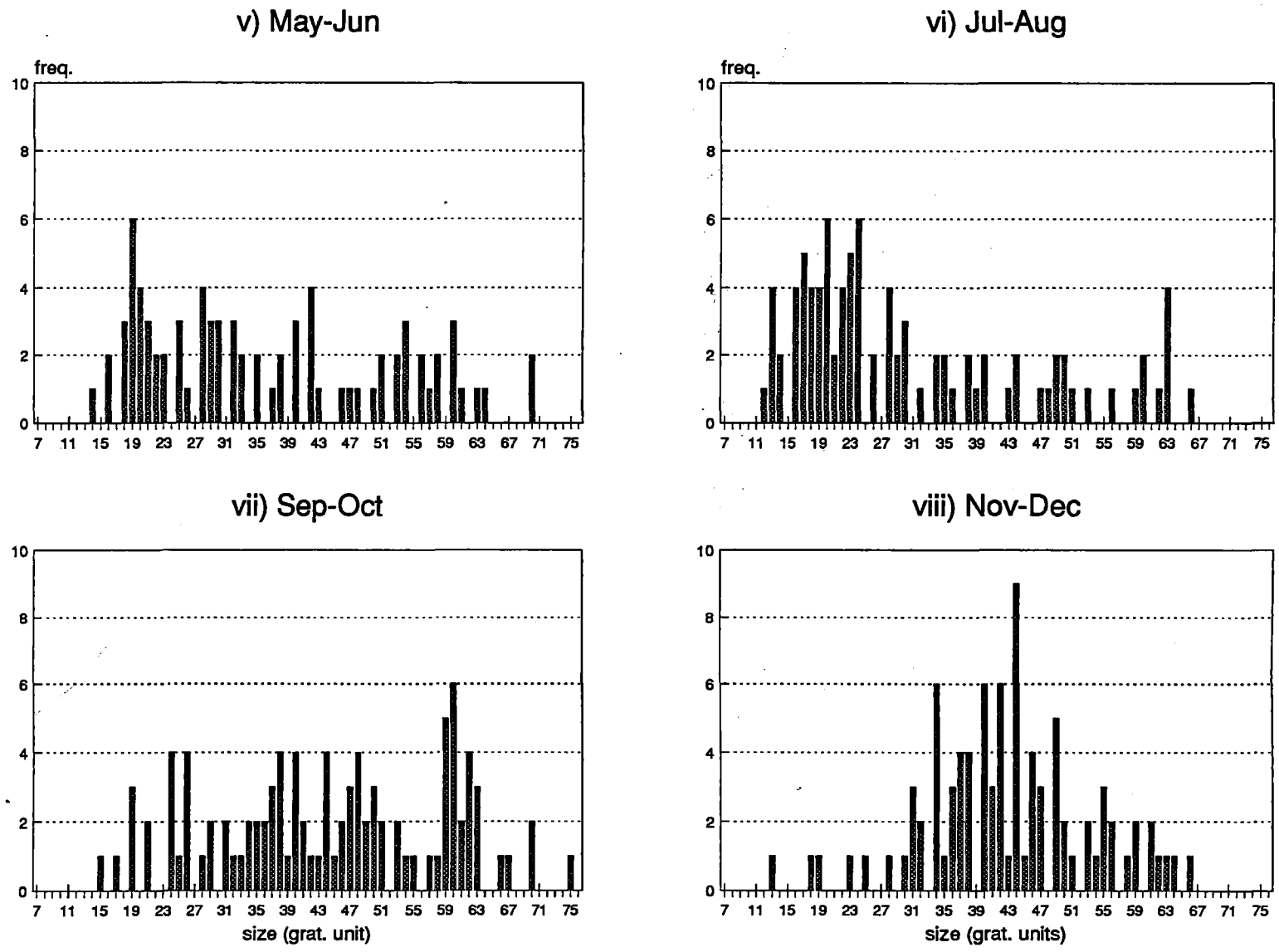


Fig. 4.9 shows two typical individuals (both female) from each size class. Fig. 4.10 is a histogram of tibia length (as a function of overall size) versus frequency. A $\chi 2$ goodness of fit test was made to determine if the data expressed in this graph were bi-modal as suspected. If the different sizes of adults encountered are the expression of typical variation (continuous distribution) in a population, one would expect the sizes to be normally distributed about a mean. The *A. ptyoptera* data set failed to fit a normal distribution model. If the different sizes are the expression of two sub-populations, as proposed, we would expect a "double normal distribution". The *A. ptyoptera* data set does fit a double normal with unequal variances distribution ($\chi 2 = 20.13$ which is less than the tabulated $\chi 2$ for 14 dof and $p = 0.05$). However, the test suffered from having some low expected values which might invalidate the test, although some statisticians suggest that the expected frequency may be relaxed in the end cells (Bhattacharya & Johnson 1977). Therefore it appears there are two size classes. The data in Fig. 4.10 is the pool of specimens from 1988 and 1989. Both years were also found to have a double normal distribution with unequal variances. This phenomenon does not appear to be related to sex or time of emergence and has been found in the collections sighted as well as my own specimens.

If *A. ptyoptera* is able to vary the number of instars undertaken, then it is a strategy that involves the trade-off of shortened developmental requirements against reduced fecundity (see Section 4.5). Such a strategy would presumably give rise to a remarkable ability to cope with a wide variety of environments and unreliable nutrient sources.

**Seasonal Strategy**

Dormancy is a concept that encompasses many states of resting, usually during a period of habitat adversity. Within the dormancy super-group, it is important to distinguish between simple quiescence and true diapause. Many examples of dormancy are cases of quiescence, since the resting stage can return to normal levels of activity as soon as conditions become favourable. By contrast, true diapause is a pause in development (Cossins & Bowber 1987). While diapause is being expressed, metabolic activity is suppressed even if conditions favourable for development occur (Tauber *et al.* 1986). Diapause is a complex, neurohormonally mediated, physiological state of increased hardiness to environmental extremes. The full (species-specific) expression of diapause usually develops in response to a combination of a number of environmental stimuli that precede unfavourable conditions, but in themselves may not be untoward (i.e., "token stimuli": usually photoperiod). Diapause is said to occur only during a genetically determined stage(s) of metamorphosis (Beck 1980), including larval diapause which usually occurs at one specific instar only (Danks 1987), but exceptions do occur (Danilevski 1965).

In addition to ensuring individual and species survival over periods of environmental adversity, diapause adaptations may also serve to synchronise insect populations so that life history episodes of individuals occur together (and at favourable periods) as well as to synchronise feeding periods with the availability of hosts (Chippendale 1982).

FIG. 4.9: Two *A. ptyoptera* females from different size classes

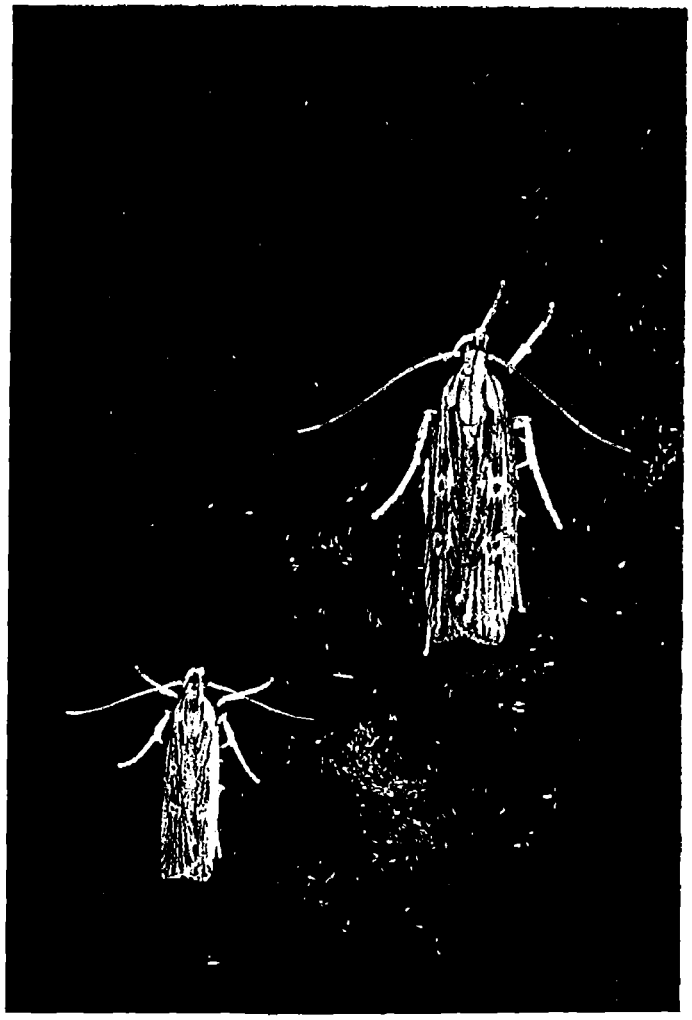
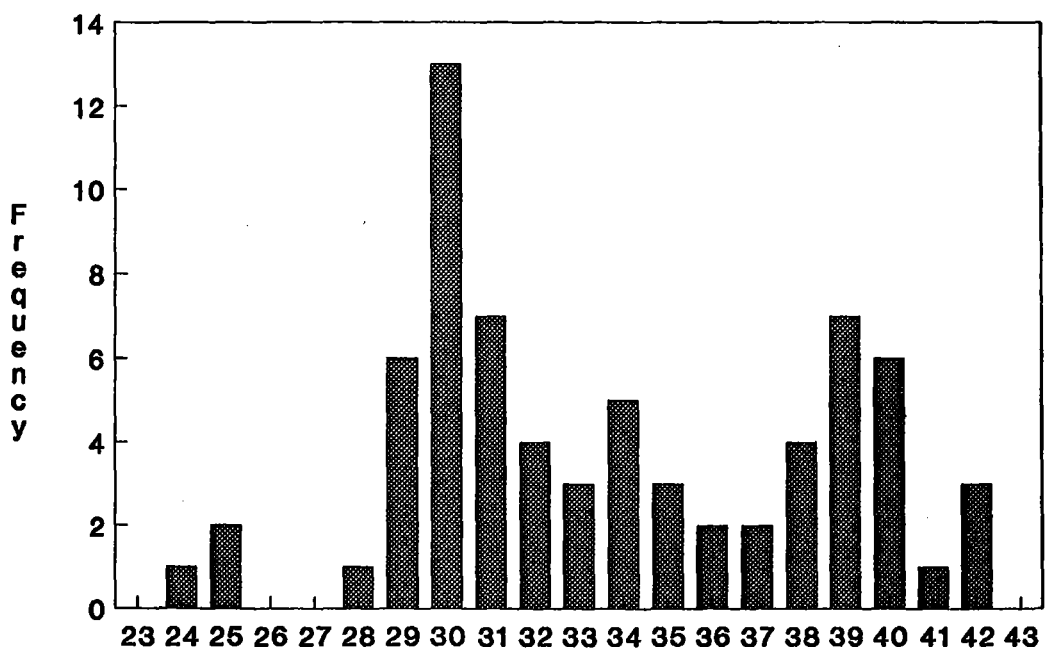


FIG. 4.10: Frequency histogram of tibia lengths of adult *A. ptyoptera* collected in this study



It was hoped that the seasonal response of *A. ptyoptera* to temperature and photoperiod could be measured using the artificial rearing exercise. However, the culturing approach was, in general, a failure. Due to malfunctions in the constant temperature cabinets used and other complications associated with artificial rearing, very few of the 1987 culture survived to pupal stage and only two adults emerged, both of which were deformed. Of the 41 larvae in the 1988 culture 15 emerged and 26 did not (four were parasitised) (see Appendix Table III.2). The high rate of mortality was due mainly to two factors; invasions of mould and the diet over drying, causing the larvae to dehydrate. (Rearing techniques are more thoroughly discussed in Section 5.3.)

As the 1987 GPD trial was to be the the experiment in which different temperature and light regimes were to be examined, no conclusions can be drawn as to the influence of these variables on the seasonal strategy of *A. ptyoptera*. However, some insight was gained into rearing this agent (the importance of which has been discussed in 2.4.2).

Because it was found that development can occur during any favourable period, it appears *A. ptyoptera* does not exhibit true diapause. Thus the over-wintering strategy of *A. ptyoptera* may be categorised as larval quiescence. A characteristic of larval quiescence is a loss of the synchronising effect of diapause. This is evident in the seasonal strategy of *A. ptyoptera*: overlapping and variable distribution of life stages. Such a strategy conforms to the model that has been proposed for most New Zealand insects as seasonal opportunists (Sutherland 1964; Dumbleton 1967; Roberts 1977). The ability of *A. ptyoptera* larvae to commence development if brought into warm temperatures during winter (with no apparent regard to photoperiod) adds further support to the opportunistic model.

However, as the photoperiodic response of *A. ptyoptera* was unable to be examined, the classification of its over-wintering strategy remains uncertain. On one hand, the diffuse life history and spontaneous development of *A. ptyoptera* more closely resemble quiescence than the traditional concepts of diapause. Further, given that *A. ptyoptera* bores in a tough substrate which has a low N content (Hill 1982), this moth may require a long period of development and there may not be time or necessity for diapause (Gibbs pers. comm.). On the other hand, the possible ability to vary the number of instars undertaken (Section 3.2) and an apparent variability in larval growth rates (noted in the artificial diet culture) point to the possibility of diapause within this moth's biology. This aspect of the study will only be resolved with exploration of diapause inducing stimuli and greater understanding and quantification of this insect's seasonal strategy.

### 4.2.4 Seasonality in New Zealand Lepidoptera: A personal perspective

The Insecta is a massively diverse class that exhibits a wide diversity of seasonal responses. Attempting to superimpose a strict classification of response types over all insects may not be wholly appropriate.

The body of knowledge concerning insect seasonality has been generated almost entirely in the USSR, North America and Europe, i.e., the temperate regions of the Northern Hemisphere. From this body of

knowledge, it appears that non-diapause seasonal responses are relatively rare and nearly all insects exhibit some form of diapause. It has thus been suggested that New Zealand insects are unusual in that no truly endemic species expresses diapause (Roberts 1978).

According to the proposal of Dumbleton (1967), the 'low incidence' of winter diapause in New Zealand insects and winter deciduousness in native dicotyledons are a result of our comparatively warm climate during the Pleistocene, when diapause was evolving in the Northern Hemisphere. Further, it has been suggested that our mild winters and the presence of a year-round food supply would make diapause an unnecessary adaptation in New Zealand phytophagous species (Watt 1975; Roberts 1978) (although food quality is likely to vary).

Most reports published before 1989 supported this hypothesis (e.g., Sutherland 1964; Spitzer 1970; Gaskin 1975b; Roberts 1977, 1978; Gibbs 1980). However, some workers suspected some indigenous diapause (e.g., Wilkinson 1964; Harris 1974). Roberts (1977) reviewed cases of over-wintering in New Zealand - most cases examined then were Lepidoptera. She concluded that there were no certain cases of truly endemic New Zealand diapause, and the evidence suggested quiescence operating, rather than diapause (in the European sense). The 1977 New Zealand Entomology Society Symposium addressed the issue of seasonality in New Zealand insects. No clear pattern was found. Ramsay (1978), Watt (1978) and Roberts (1978) found diapause did not exist in the groups they studied, but Deacon (1978) and Young (1978) suspected diapause.

In general, these earlier studies were field-based, and critical experiments to determine if photoperiod and/or temperature are involved in inducing a diapause response were not done. To understand seasonality, all relevant parameters need to be systematically surveyed (Danks 1978). At present, only a few New Zealand insects have been studied in sufficient detail to distinguish the actual type of dormancy and the affecting factors.

Recently Morris (1989) reviewed the evidence for diapause in New Zealand insects. He cited three studies that demonstrated photoperiodic response in species of New Zealand Lepidoptera and suggested that this might be evidence for diapause occurring.

Determination of when diapause begins and ends in laboratory and field populations of insects may be difficult (Tauber & Tauber 1976). Possible indicators of diapause in Lepidoptera include the following:
i) diapausing individuals may undergo extra instars (e.g., Chippendale & Yin 1973; Rock & Shaffer 1983; Oku 1984); and
ii) a prolonging of larval instars may also be part of diapause (Rock & Shaffer 1983).
Although using these expressions in diapause studies ignores more reliable physiological monitoring, they have been taken to be reasonable assumptions that provide accessible indicators of diapause. By using these indicators, recent laboratory studies have indicated that diapause may be expressed in some New Zealand Lepidoptera (Muggleston 1989; Morris 1990; Gibbs unpub.).

The laboratory studies of Muggleston (1989) and Morris (1990) both demonstrate a prolonging of larval instars at certain photoperiods. Muggleston (1989) used the measure 'not pupated after 12 weeks of larval development' at 18°C. She found *Stathmopoda aposema* (Meyrick) (Lepidoptera: Oecophoridae: Stathmopodinae) exhibited a "long-day/ short-day" (*sensu* Beck 1980) response. Morris (1990) recorded the duration of all instars and the number of instars required before pupation in *Planotorix excessana* Walker (Lepidoptera: Tortricidae). The response expressed (increase in the number of larval moults and larval duration) corresponds to a "long-day" response with a critical daylength around 14-15 hours at 21°C. Although these studies do not prove that diapause is occurring, the evidence does point to a diapause mechanism being involved.

Within the New Zealand Lepidoptera, there appears to be a regularly occurring theme: wide individual variation in the rate of development in the stages during or succeeding over-wintering, sometimes expressed as two portions of the population. For example, Muggleston (1989) reported that considerable variation between individuals is superimposed on the response of *S. aposema* to photoperiod. At 18°C only about 60 percent of the population expressed the photoperiodic response noted, while the remaining individuals presumably continued development. Strong influences of diet and temperature were also noted. Gibbs (unpub.) examined wild populations (cf. Morris 1990) of New Zealand copper butterflies (*Lycaena* spp.). Like Muggleston, Gibbs found that in response to photoperiodic cues, there is variation in the larval period within populations (diapause individuals have a pause in development). Similar findings have also been reported by Wilkinson (1964) - two fractions in a identically treated *Metacrias strategica* (Meyrick) (Lepidoptera: Arctiidae) population as distinguished by variation in the rate of growth in the over-wintering larvae in each fraction; and by Gaskin (1975b) - large variation in the duration of the final instar in over-wintering *Oracrambus vitellus* Doubleday (Lepidoptera: Pyralidae).

As discussed in Section 3.2, variation in the development rate and number of instars undertaken by *A. ptyoptera* larvae may also occur, although development of individuals was not measured directly. A possible reflection of a development polymorphism is the broad range of larval size at all times of the season (Fig 4.7). However, the cause of this spread and the absolute age of the larvae within these graphs is unknown. More convincingly, the growth rates of the larvae in the culturability trial exhibited considerable variation (Appendix Table III.2) (all were kept in identical conditions), although too few specimens survived to make this a conclusive observation.

Although the New Zealand climate has distinct seasons, abrupt unseasonal fluctuations of temperature and humidity are common (cf. continental stability) (Garnier 1950; Hurnard 1978; Goulter & Hurnard 1979). Therefore photoperiod in New Zealand may not be a highly reliable seasonal cue, as opposed to Northern Hemisphere continental situations. This unpredictability may be the evolutionary drive causing:
i) the highly variable seasonal responses (including response to photoperiod);
ii) our insects' apparent sensitivity to fluctuations in other ecological variables (not necessarily climatic adversity) e.g., the apparent sensitivity of *Wiseana* spp. to small atmospheric ion activity (Helson &

Penman 1970), circadian rhythms (e.g., Roberts *et al.* 1983), as well as temperature (e.g., Muggleston 1989); and

iii) a high degree of spontaneous exploitation of favourable conditions when and where they occur, combined with a readiness to quiese when necessary (e.g., Sutherland 1964).

This spontaneity and sensitivity to a wide variety of stimuli, combined with variable growth patterns, may constitute species "hedging their bets". Having a non-diapause fraction in the population may enable the exploitation of early or late favourable conditions and hence facilitate population growth, while the diapausing individuals would ensure survival in less favourable seasons (e.g., Palmer 1982). Under these circumstances we would expect high variation in response to photoperiod, which would be maintained by shifting selection pressures (Dingle 1984).

The evidence presented above is far from conclusive, partially because so few cases have been examined and partially because variation in larval development and the number of moults can be caused by many variables besides seasonal responses. However, the evidence does allow a hypothesis to be constructed: a diapause mechanism may operate in at least some species of New Zealand Lepidoptera. In the species reviewed, part of their over-wintering strategies may be a variable growth rate response. This could possibly sub-divide the population into two parts and thus give rise to two generations in a favourable season (Wilkinson 1964). Yet these cases of suspected diapause do not satisfy the traditional definition because:

i) it can, in some cases, be terminated if conditions are favourable;

ii) it involves more than one stage of morphogenesis; and

iii) it does not synchronise the population.

The popular concepts of diapause are derived from Northern Hemisphere research. These concepts do not appear to be appropriate to classify over-wintering strategies of New Zealand insects accurately. In New Zealand Lepidoptera these strategies include:

i) possible sensitivity to photoperiod;

ii) variable life stage expression;

iii) wide variation of expression within each species; and

iv) non-synchronised development.

Therefore I propose: these strategies may constitute a unique type of diapause that falls within the New Zealand model of seasonal opportunism and flexibility.

On the other hand, these responses may be simple quiescence with succeeding variable growth rates, which may be partially influenced by photoperiod, as well as other variables (i.e., temperature and food quality are likely to decline as photoperiod becomes shorter). Close physiological monitoring (of oxygen consumption, fat bodies etc.) is required to solve this puzzle.

The combination of the lack of study of phenology in New Zealand entomology and the complexity of the subject, make it currently impossible to generalise about seasonality in New Zealand insects. There is a clear need for accurate determination of the nature of seasonal responses and the examination of many more species.

### 4.2.5 Sub-Section Summary

*A. ptyoptera* over-winters as larvae and appears to be univoltine. Considerable variation was found in the seasonal distribution of life stages.

It is suggested that the seasonal strategy of *A. ptyoptera* is that of an environmental/seasonal opportunist.

Because photoperiodic response was unable to be examined in this study, the classification of the over-wintering strategy of *A. ptyoptera* is considerably less than certain. Although some aspects of this moth's biology point to the possibility of diapause, other features suggest that diapause is not expressed.

While variation in diapause depth and duration occur in Northern Hemisphere insects (Tauber and Tauber 1976, Tauber *et al.* 1986), especially in response to uncertain environments (Dingle 1984), in New Zealand Lepidoptera, the variation shown in the over-wintering response combined with life history spontaneity is not consistent with the traditional definition of diapause. However, the occurrence of photoperiodic response, variation in the number of instars undertaken and variation in larval duration, all suggest some form of diapause response is occurring.

If diapause is occurring in New Zealand insects, it appears to be part of a very flexible set of strategies that make up their life histories - a complex set of adaptations for spatio-temporal uncertain environments (Dingle 1984).

## 4.3 Larval Feeding Sites and Behaviour

### 4.3.1 Introduction

The larval period in the life cycle of all endopterygote insects is predominantly a time of feeding and growth. *A. ptyoptera* larvae are behaviourally and morphologically (Section 3.1) adapted to feed and develop within the woody stems of their hosts.

Weed biocontrol theory has for many years placed an order of significance on the structures of the target a potential agent attacks, i.e., roots-crowns > structural elements > foliage > reproductive structures (Harris 1973; Goeden 1983; see review in Hokkanen 1986). This assessment scheme has been used in assigning priorities among gorse control agents (Hill 1983). However, recently this theory has been questioned (Hokkanen 1986; Crawley 1989a, c), and any damage inflicted on the host may be significant (Harris 1981a) (see Section 2.4.2). Nevertheless, the structure which a phytophagous agent attacks will be one of the primary determinants of its effect, and is therefore considered in assessing any biocontrol agent.

One of the objectives of this study has been to ascertain the general biology of the larvae. This included examining how the young larvae become established in the stem, which tissues and structures of the plant *A. ptyoptera* attacks, and what the mode of attack is. These aspects are discussed in this chapter. Other aspects of larval biology, *viz.*, incidence of parasitism and the instar determination, are discussed in Sections 4.4 and 3.2 respectively.

### 4.3.2 Materials and Methods

Southwood (1973) argued that there were at least three major "hurdles" to overcome before insects could successfully exploit plants. These hurdles are nutrition, attachment and desiccation difficulties. As *A. ptyoptera* is a stem-miner, attachment and desiccation problems are presumably largely overcome. However, stem-mining poses a further difficulty in that a newly emerged larva must get from the surface of the plant, where the egg was laid, into the interior of the stem.

The manner in which newly emerged larvae enter the stem was examined by placing 10 eggs on two small gorse bushes. After three weeks the bushes were carefully dissected and the route of entry ascertained.

The proportion of larvae that become established was also examined. Seven, 10, 15 & 30 eggs were placed in gelatine pill capsules attached to separate plants (two replicates) in January 1989. The plants were kept in a glasshouse to prevent inoculation by wild *A. ptyoptera*. The glasshouse was unheated and had natural light. In November 1989 the plants were dissected and the number of individuals established and the life stages achieved recorded. Gorse plants do not survive well in artificial conditions; this, added to the pressure of *A. ptyoptera* attack, caused several of the plants to die before the end of the experiment. They were dissected as soon as they died.

Data concerning which part of the target is attacked were gathered in the sample effort described in Section 4.2. For each larva found, its position in the plant (i.e., the age of the wood it occurred in) and whether the larval gallery occurred as a "mine" (under the bark) or a "tunnel" (along the pith) was recorded, along with the date and locality of the collection.

The system for referring to wood age groups of gorse foliage has been discussed in Section 4.2.2. Because *A. ptyoptera* was not often found in wood over four seasons old (i.e., G4), "branches" were only sampled to G4. The distribution of larvae within gorse bushes (G1 to G4) is recorded in absolute numbers and plotted in the frequency histogram in Fig. 4.12. Occasionally (15 out of 418 cases), galleries were found to occupy more than one age class of wood, but these records were not included. Galleries containing parasites or no occupants ("abandoned") were also omitted.

The tissues that the larvae feed in were investigated by first determining the cellular arrangement within the gorse stem and then, by dissection and exposing larval galleries, the tissues that the larvae were feeding in were ascertained.

The arrangement of tissues within gorse stems was examined by taking a small, thin transverse section by hand using a "Gem" single edge razor blade. The section was then thoroughly washed in water, placed in a dilute Toludine Blue solution for one minute, washed again and then mounted in dilute glycerine. The resultant slide was viewed under a Reichert (Nr 64683) compound light microscope. The film used for the photomacrography was Ektachrome Tungsten balanced EPT, 160 ASA.

### 4.3.3 Results and Discussion

Observations from the fecundity, host specificity and field monitoring exercises suggest that oviposition occurs on almost all aerial parts of the plant. However, there appears to be a preference for laying in the gap between the leaf and its associated stem. Recently eclosed larvae are highly mobile, and often migrate by walking or dropping on silken threads to other parts of the plant. It appears the most common establishment site is through vegetative buds in the axils of woody stems. The larvae eat into the soft tissue and enter the phloem-cambium region directly under the bark. An exposed early gallery around a primary spine is shown in Fig. 4.11. Another frequent establishment site is through old wounds in the stem from previous galleries. Occasionally larvae were found to have entered the stem directly through the bark.

**G. 4.11: An exposed early *A. ptyoptera* larval gallery around a primary spine on a gorse branch. The most common site of initial establishment is through the vegetative buds between leaves and stems.**

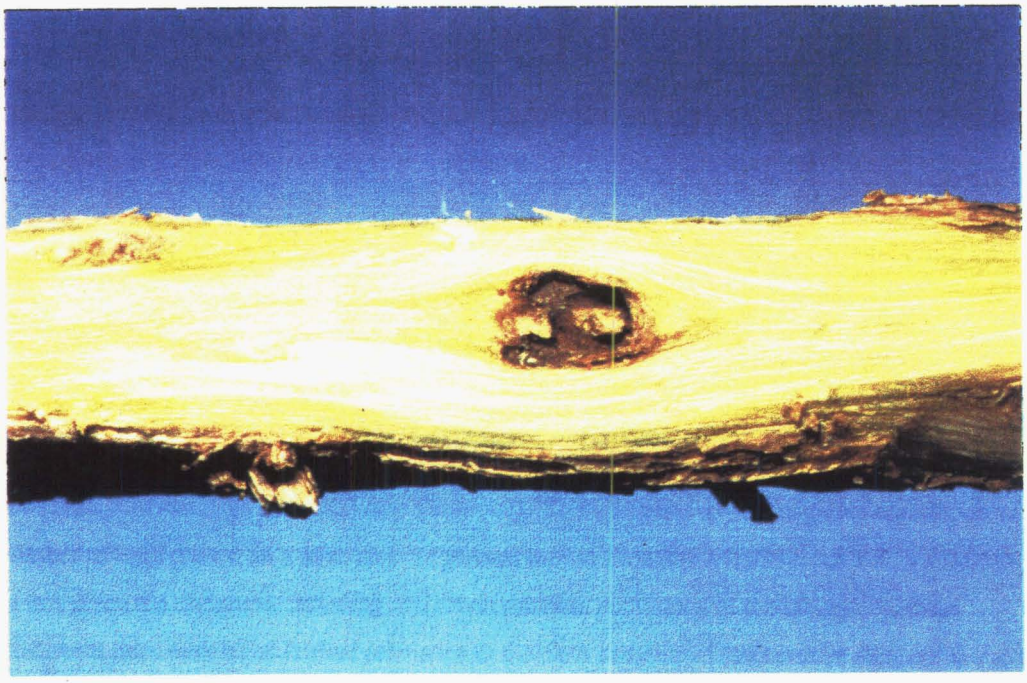


**FIG. 4.13: A cross section of a gorse stem showing an *A. ptyoptera* larval gallery. *A. ptyoptera* feeding appears to mostly occur in the phloem-cambium region of the host.**

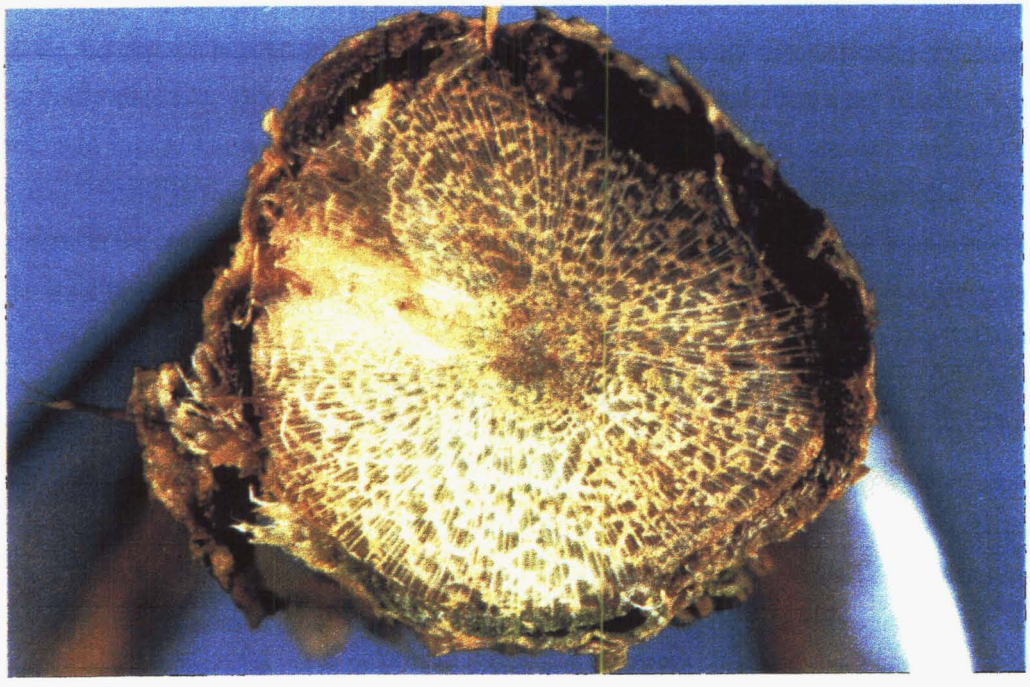


**TABLE 4.2: *A. ptyoptera* larval establishment under various crowding regimes.**

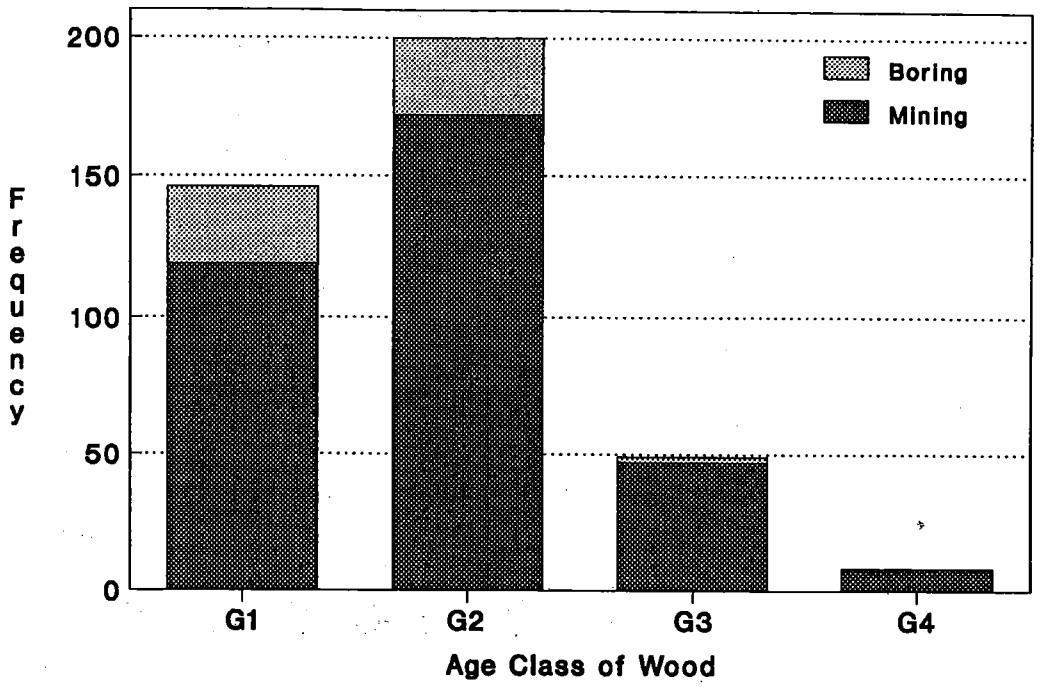
| Eggs per bush | Number of larvae estb. | % estb. | Most advanced life stage |
|---|---|---|---|
| 6 | Plant died | | |
| 7 | 6 | 85.7% | Instar V? |
| 10 | 7 | 70% | Plant died |
| 10 | 7 | 70% | Instar III? |
| 15 | 7 | 46.7% | Plant died |
| 15 | 6 | 40% | Adult |
| 30 | Plant died. | | |
| 30 | 5 | 16.7 | Adult |

On the artificially inoculated plants, initial establishment ranged from 16.7 percent (30 eggs per small bush) to 85.7 percent (seven eggs per bush) (see Table 4.2). There appears to be a negative correlation between the number of eggs placed on a bush and the percent establishment ($r = 0.9394$, $dof = 4$, $p = 0.05$). However, given the unnatural crowding and environmental conditions of the laboratory, these establishment rates may be of limited relevance to the field situation. Observations suggest: i) if given space, moderate temperatures and sufficient humidity (i.e., supposedly natural conditions for a nocturnally active inhabitant of dense foliage), *A. ptyoptera* females scatter their egg load in time and space and lay eggs singly (Hill & Holder unpul. obs.); and ii) the degree of wind exposure appears to influence female flight and oviposition behaviour, and hence the distribution pattern of the population.

The poor flying ability hypothesis is supported by the marked difference in the distribution pattern of *A. ptyoptera* at the Burnham and Taitapu field sites. Although the distribution patterns were not statistically tested, the *A. ptyoptera* population at the sheltered Burnham site appeared to be uniformly distributed among nearly all plants. This contrasts with the population at the exposed Taitapu site (see Fig. 4.2). The population at Taitapu was distinctly clumped, with 48 percent of the plants not attacked (see Section 5.2). Further, at Taitapu, groups of up to eight individuals, believed to be from the same oviposition event, were often found in the same section of wood, but this phenomenon was found only once at Burnham. Given that the females seem to have limited flying ability, it is suggested that windy conditions at Taitapu often confine the females to a single bush, or at least, limit their dispersal of eggs. However, as noted in Section 4.2, there are many variables that are unequal between the sites which necessitates a cautious interpretation of any inter-site comparison.

Presumably the position in which a stem-borer occurs within a plant will influence the impact it has upon its host. The larval feeding positions of *A. ptyoptera* are shown in Fig. 4.12. Fig. 4.12 shows that the most frequent site of occurrence is G2 (47.8 percent) and most (85.6 percent) of the feeding sites are in G1 & G2. Because there are more G1 & G2 branchlets in a bush than G3 & G4, no conclusion can be drawn about the

FIG. 4.12: Frequency histogram showing the distributiom of *A. ptyoptera* larvae in different growth stages of gorse foliage



preferred feeding site without weighting the results to take into account the different amounts of each wood class sampled. However, the objective of this study was merely to see where the larvae occur and the amount of each wood age group that was examined was not recorded.

Fig. 4.12 is misleading in that it does not show that feeding occurs in all woody parts of the plant, including the crown and wood older than G4; also, it does not indicate the impact of feeding. The age of attack is suspected to influence the degree of damage inflicted on the host. However, possibly due to inappropriate technique, no reliable correlation between the age of attack site and the degree of damage inflicted was found (see Section 5.2).

Besides G1 & G2 branchlets being encountered most frequently, other possible reasons for most of feeding occurring in G1 & G2 include: i) nutritional advantages of feeding nearer the terminal segments (Rhoades & Cates 1976; Rhoades 1979); and ii) because of the dense growth form of gorse, access to the outer branches may be less restricted (for both adults and larvae).

Fig. 4.12 does not include the "abandoned" galleries. Galleries with no occupants and no sign of occupant demise were regularly found. These ranged in size from 3 to 25 mm long. Given the dangers of predation and desiccation a wandering larva would face (Strong *et al.* 1984), the occurrence of these unoccupied galleries is perplexing. Possible explanations for this behaviour include:
i) some influence of natural enemies; or
ii) if the host becomes unsuitable, larvae may leave their galleries, re-establish and commence development in another gallery. Larvae that had abandoned their galleries were often found wandering on branches which had been cut and brought into the laboratory; since *A. ptyoptera* often weakens and sometimes kills its host, the larvae may be sensitive to host deterioration. Conversely, in cut stems used in other experiments, although several wandering individuals were found, many larvae were found that did not leave their galleries and died with their host stems (see Table 4.4). This suggests that larvae do not necessarily act upon host deterioration.

It was found that 86 percent of the larval feeding occurred as "mines" (see Fig. 4.12), i.e., in the zone immediately below the bark. From examination of the arrangement of cells in gorse stems, it was concluded that *A. ptyoptera* larvae predominantly feed in the phloem and cambium tissues (Fig. 4.13). This strategy has possibly arisen to meet some of the nutritional difficulties of herbivory.

The available nutrition (especially N) in plant material is often close to or below phytophages minimum requirements (Mattson 1980). The evidence for the role of nitrogen in insect-plant relationships has been reviewed by McNeill & Southwood (1978), White (1978), Onuf (1978) and Mattson (1980). There appear to be three themes involved in the relationship of plant N and herbivory.

i) The quantity and form of proteins and amino acids in phytophages' diet influences their development and reproduction (McNeill & Southwood 1978) and plants will obviously suffer if insect reproduction is high.

Yet the composition of plant and animal tissues are very different: plants consist mainly of carbohydrates, whereas animals consist largely of protein (DeFoliart 1975). Hence N is scarce and perhaps a limiting factor for many herbivores.

ii) The selective pressures of herbivory appear to have resulted in "apparent" plants (*sensu* Feeny 1976: long lived and growing in association with others of the same species) utilizing a) the non-availability of proteins and amino acids as a defence mechanism (Moran & Hamilton 1980); and/or b) having the flushes of N as short and unpredictable in time as possible (McNeill & Southwood 1978). Gorse is a plant which uses physical and low N defence strategies. Mature gorse is very prickly, and the function of surface trichomes (Zabkiewizc & Gaskin 1978) and cuticle toughness (Hill pers. comm.) may be to hinder insect establishment. Further, gorse does not appear to employ metabolically expensive "secondary (anti-herbivore) compounds", but employs the strategy of having a low N content except during the brief flush of spring growth (Hill 1982).

iii) Scarcity of N has in turn been a selection pressure on herbivores. Phytophagous insects have evolved specific behavioural, physiological, phenological, morphological and other adaptations to cope with and utilize low or variable levels of usable N in their host plants. These adaptations include:
a) The synchronisation of life histories so that periods of maximum feeding coincide with flushes of N (i.e. bud-burst, growth phases). For example, the larvae of *Agonopterix ulicetella* emerge just as the new growth of its host, gorse, begins (Hill 1982).
b) Variable feeding rates and efficiencies of digestion; and/or
c) Prolonged periods of feeding and development (Mattson 1980).
d) Specialised digestive systems that rely on endosymbionts (Koch 1967).
e) Occasional carnivory; cannibalism or predation (Mattews 1967).
f) Feeding in N rich parts of the plant (e.g., actively growing tissue and storage tissues).

As the larvae of *A. ptyoptera* were found to mine mostly in the phloem-cambium region of their hosts, it is suggested that this insect exploits the most reliable source of N (and possibly other nutrients) in an otherwise deficient host. The cambium is actively dividing tissue and hence N rich, and phloem sap contains between 10 and 100 times more N and about 1000 times more sugar than xylem sap (Mattson 1980). It was also found that a common mode of attack is to girdle the stem and hence ring-bark the branch. Given the vertical movement of phloem sap, girdling maybe a strategy that is employed so that the larva connects with the maximum nutrition (phloem sap).

The larvae boring in the pith almost always had much longer galleries (up to 350 mm). This may be due to a lower food quality and/or a reduced resistance of this tissue.

As the larvae develop and become larger, their galleries occupy a greater proportion of the stem. Hence the larger the larva the greater the restriction of the transport elements. As a result, although damage to gorse

occurs at all times of the year, it is most visible as the mean larval size peaks from September to December (see Fig. 4.8).

A further behavioural feature of *A. ptyoptera* appears to be a prolonged period of feeding and development. This is possibly coupled with a complex seasonal life strategy that may involve development polymorphism (see Section 3.2 & 4.2) and/or variable rates of feeding or development. It is quite likely that the life history strategy of *A. ptyoptera* is linked to the nutritional restrictions of its diet; the long feeding period may be necessary to complete development in a hard and nutritionally deficient host.

### 4.3.4 Sub-Section Summary

*A. ptyoptera* is a stem miner. Larval feeding structurally weakens the host and disrupts vascular transport. Eighty-five point six percent of larvae occurred in wood one and two growth seasons old. Eighty-six percent of the feeding galleries were found in the cambium-phloem region of the stem. It is suggested that this is a strategy to overcome a shortage of N (and possibly other nutrients).

## 4.4 Incidence of Parasitism

### 4.4.1 Introduction

Parasitic insects that attack invertebrates nearly always destroy their hosts (Askew 1971), and can be described as parasitoids. The term "parasitoid" was introduced by Reuter (1913 - cited in Waage & Greathead 1986) to describe a life style between that of predators and true parasites. Adult parasitoids are free-living and forage actively for their hosts on plants or other substrates. Usually the female lays one or more eggs in (endoparasites) or on (ectoparasites) the host, and the ensuing larvae consume the host tissue, killing the host in the process (Waage & Greathead 1986). Most parasitoids belong to either of the two large orders: Hymenoptera and Diptera (also Coleoptera, Lepidoptera and Strepsiptera) (Clausen 1962). The majority of parasitoids are endoparasitic, and their larvae have, in most cases, adapted to living in a mass of semi-liquid food. Further information on insect parasites can be found in the excellent book by Askew (1971) and in the reviews by DeBach (1974), van den Bosch *et al.* (1982), and Waage & Greathead (1986).

All insects have their complex of parasites and predators (Early 1984), and although assessing the impact of natural enemies is difficult, they are likely to have an important restraining effect on most populations (DeBach 1964; Huffaker 1971; Huffaker & Messenger 1976; Huffaker *et al.* 1984).

Recently the importance of natural enemies in structuring some animal communities has been questioned. Current theory says that it is doubtful if parasitism "regulates" populations (of Lepidoptera at least) (Dempster 1983). Indeed, field data tend to suggest that the "regulation about an equilibrium" hypothesis is inappropriate for natural populations, and more random models of fluctuations between "ceiling" (resource depletion) and "floor" (extinction) may, in most cases, be more applicable (Strong 1984).

Nevertheless, natural enemies can limit insect populations (Hassell 1986) and their effect is likely to be critical on small, vulnerable founding populations (Lawton in press). Therefore one of the desirable characteristics of a biocontrol agent is low susceptibility to generalist mortality agents (see Section 2.4).

Phytophagous insects that are introduced as biocontrol agents against weeds are often attacked in their new home by native parasitoids (Goeden & Louda 1976). These parasitoids are usually recruited from the natural enemies of ecologically similar insects (Lawton 1986). This appears to be because habitat selection is a large component of host selection for many hymenopterous parasitoids, and hence they will attack a variety of host species provided that they all feed on the same species of plant (Picard & Rabaud 1914 - cited in Thorpe & Caudle 1938?). (This gives rise to the question: did *A. ptyoptera* parasites make a habitat/host plant switch with *A. ptyoptera* or did parasites of gorse stem borers get recruited? This very interesting issue was beyond the scope of this study.)

Although it is believed that native parasitoids can and do prevent establishment (Goeden & Louda 1976), Lawton (1986) found no records that show parasitoids have actually prevented a species from establishing. However, given the extreme difficulty of determining why biocontrol programmes fail, the lack of data does not prove that native parasitoid attack cannot cause extinction of founding populations. On the other hand, predation of founding populations has often been implicated as causing establishment failure (Goeden & Louda 1976; Crawley 1987). Disease is thought to be the natural enemy least likely to prevent establishment (Crawley 1986).

Ideally, liberating *A. ptyoptera* in a place without specific parasitoids would result in successful and rapid establishment, a large population and therefore high levels of damage to gorse (see Section 5.2). However, evaluation of the eventual influence of novel natural enemies cannot be attempted.

Butler (1979) suggested that there are parasites that attack *A. ptyoptera* and that they may have been responsible for periodic crashes of local moth populations that he suspected. The nature of these parasites was not indicated. Given the probable importance of parasites to the possible establishment and performance of *A. ptyoptera* as a biocontrol agent, aspects of its parasitoid complex were examined. The purpose of this examination was three-fold:

i) to determine the identity of *A. ptyoptera* parasitoids and which life history stages they attack;

ii) if the identity could be determined then the specificity of the parasitoids could be estimated by literature search (considered important because of the desirability of not being attacked by generalists); and

iii) the isolation of the parasitoids would enable me to ascertain if any of them are known to exist in Hawaii.

A further objective was to measure, if possible, the percent parasitism of a single generation, and thereby estimate the impact of parasitism on *A. ptyoptera* populations.

### 4.4.2 Materials and Methods

**Eggs**

Through earlier observations, it was suspected that *A. ptyoptera* eggs are parasitised by a trichogrammatid (Hill pers. comm.). Occasionally, eggs were found on the field samples described in Section 4.2. The location of these eggs was noted and they were kept at room temperature to monitor the emergence of parasites.

**Larvae**

During the preliminary investigation, empty pupal cocoons of a unknown ichneumonid and pupae of an unknown chalcid were found in *A. ptyoptera* galleries in association with larval remains. These observations confirmed the occurrence of larval parasitism, and further investigation was undertaken to isolate specimens of these parasites and estimate percent parasitism. Eventually four different techniques were used:

i) Larval galleries and their contents were monitored weekly (described in Section 4.2);

ii) *A. ptyoptera* infested gorse branches were caged *in situ* using nylon gauze sleeve cages from late spring to mid summer;

iii) Sections of infested branches were placed in lidded battery jars in early summer (Fig. 4.14).

iv) In the first week of December 1987, 25 infested branches were collected from each of the Burnham & Greenpark (map reference: M36 685228) field sites. The branches were de-spined, then enclosed in two perspex incubators (see Fig. 4.15). To increase the humidity inside the incubators, a dish of water was placed in each. After nine weeks all insects had stopped emerging from the branches. The branches were dissected to find the number of pupae (emerged and unemerged), parasite remains and unemerged larva. Previous season's pupae and parasite exuvia can usually be differentiated from the current season's, therefore error due to inclusion of data other than the current season's should be minimal.

The parasitoids reared from *A. ptyoptera* larvae were sent to specialists for identification. The adult parasites were measured from the front of the head to the tip of the abdomen. The parasite particulars for each month are recorded in Appendix Table III.1.

**Pupa**

Over the course of the study, 78 *A. ptyoptera* pupae were found in the field (not including those in the branches used in the enclosure experiments). These were brought into the laboratory and placed in Samco flat bottomed glass tubes (75 x 25 mm) that were then stopped with cotton wool. The pupae were generally kept in their pupal galley with the bark tied back over them.

The pupae were maintained at room temperature (mean approximately $20^0$C; range: 14-30) in a small cupboard that also contained a dish of water. The timing of their emergence was noted and the resultant adults were used in the fecundity and host specificity trials (Sections 4.5 & 5.4).

### 4.4.3 Results and Discussion

No egg parasitism was found: all four eggs found in the field produced healthy neonate larvae. Hill (pers. comm.) records that he reared parasitoids from a suspected *A. ptyoptera* egg, but neither the eggs nor the parasitoids now exist. Hence *A. ptyoptera* eggs are possibly parasitised, but because the evidence is both insufficient and, in the case of Hill (pers. comm.) not definite, the existence of egg parasites is uncertain.

Given that *A. ptyoptera* eggs may be susceptible to parasitoids, they could be parasitised in Hawaii. The polyphagous egg parasitoid, *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) is known to exist in Hawaii (Goeden & Louda 1976). However, the occurrence of this and/or other egg parasites in gorse is not known.

No evidence of pupal parasitism or predation was found in either the pupal enclosure experiment or in the weekly field surveys. Pupal parasitism, if it occurs, must therefore be minimal in *A. ptyoptera* populations in Canterbury.

**FIG. 4.14: Lidded battery jar as used to collect specimens from sections of *A. ptyoptera* infested gorse branches**

**FIG. 4.15: Perspex incubator as used to contain whole *A. ptyoptera* infested gorse branches for i) the collection of parasitoid specimens; ii) the estimation of percent parasitism; and iii) the collection of *A. ptyoptera* adults.**

Given that the same species of parasitoids emerged both from isolated *A. ptyoptera* larvae in the diet trial (see Section 5.4) and from the branches in the enclosure experiments, it is assumed that the parasitoids that emerged in the enclosure experiment were from *A. ptyoptera* and not from subsequent Lepidopterous occupants of *A. ptyoptera* galleries (e.g., *Erechthias fulguritella* - determined by J.S. Dugdale).

Of the four approaches employed to examine the incidence of larval parasitism, sleeve caging was the least effective. Because spiders were often unintentionally enclosed within the cage, very few good parasitoid or moth specimens were recovered and no estimate could be made of the degree of parasitism.

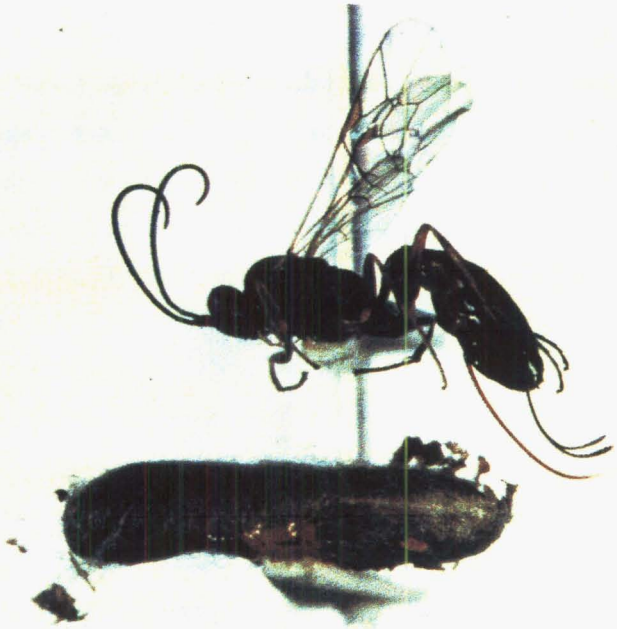
From the weekly field monitoring, specimens of two undescribed species of larval parasitoid were recovered. These were *Zealachertus* sp. (Chalcidoidea: Eulophidae), det. Z. Bouček; and *Diadegma* sp. (Hymenoptera: Ichneumonidae), det. M. G. Fritton. Because parasitised and non-parasitised larvae in the field samples could not be distinguished, it was not possible to estimate percent parasitism by the simple collection of larvae.

The smaller and less abundant of these parasitoids is *Zealachertus* sp. (Fig. 4.16). It is believed to be endoparasitic, in contrast to most species in the Eulophinae which are generally ectoparasitic (Bouček 1988). Adult females are approximately 4.5 mm long. *Zealachertus* sp. is a gregarious parasite - between 4 and 15 pupae were found in each host gallery. *Zealachertus* sp. pupae are naked and the emerging adults remain in the larval gallery for a while. The pupa were found from April to December and the adults occurred from September to January. However, the phenology of this species was not further determined. Their life history strategy appears to be to wait in the host gallery and emerge when suitable hosts are available. The emergence of the adult parasite is roughly synchronised with the adult moths (see Section 4.2); hence it is suspected that early instar larvae are the targeted stage, although it is possible (but unlikely, given the parasite's size) that they oviposit in the eggs and develop in the larvae (Bouček 1988). *Zealachertus* is a genus endemic to New Zealand (Bouček 1988), therefore with proper quarantine *A. ptyoptera* populations will be free of this parasite in Hawaii and/or other places of introduction.

The other larval parasite, *Diadegma* sp. (Fig. 4.17) is a solitary endoparasite and its pupal cocoon (see Fig. 4.17) is found inside the host gallery in association with the host larva remains. Adults appear to leave the gallery upon emergence. Female *Diadegma* sp. are approximately 8 mm long. Pupal cocoons were found from August to February and adults were observed from November to January, but a subsequent study has revealed they occasionally occur until April (Hill *et al.* unpub.). As with *Zealachertus* sp., the phenology of *Diadegma* sp. was difficult to interpret. Ichneumonids are known to oviposit in early instar host larvae (Valentine 1967) which suggests the oviposition period is December to March (see Fig. 4.8 for season distribution of the larval sizes). Thus *Diadegma* sp. appears to have a flexible life history similar to that of its host.

**FIG. 4.16: Adult *Zealachertus* sp. This gregarious parasitoid was found to parasitise up to 5.7 percent of *A. ptyoptera* larva.**

**FIG. 4.17: Adult *Diadegma* sp. and its cocoon. This parasitoid parasitises between 33.3 and 44.7 percent of *A. ptyoptera* larva.**



Because both parasites are undescribed species, an investigation of host records could not be made. Hence no conclusion can be made regarding their host specificity or habitat range.

**TABLE 4.3: Recorded *Diadegma* spp. of New Zealand and Hawaii and their hosts. *=endemic to country. SOURCES: Valentine & Walker (in prep.); Townes *et al.* (1961); this study; E. Yoshioka (pers. comm.)**

| Country | Name | Recorded Host(s) |
|---|---|---|
| **New Zealand** | | |
| | *Diadegma agens** | Not known |
| | *Diadegma fenestralis* | *Plutella xylostella* (Hyponomeutidae) |
| | *Diadegma mulleri** | *Morova subfasciata** (Thyrididae) |
| | *Diadegma semiclausen* | *Plutella xylostella* (Hyponomeutidae) |
| | *Diadegma* sp.* | *Plutella xylostella* (Hyponomeutidae) |
| | *Diadegma* sp.* | *Anisoplaca ptyoptera** (Gelechiidae) |
| **Hawaii** | | |
| | *Diadegma blackburni** | *Oeobia despesta** (Pyralidae) |
| | | *Oeobia constricta** (Pyralidae) |
| | | *Genophantis iodora** (Pyralidae) |
| | | *Hedylepta monogona** (Pyralidae) |
| | | *Spheterista infaustana** (Tortricidae) |
| | | *Phthorimaea* sp. (Gelechiidae) |
| | *Diadegma insularis* | *Plutella xylostella* (Hyponomeutidae) |
| | | *Hellula undalis* (Pyralidae) |
| | *Diadegma pattoni* | *Herpetogramma licaarsisalis* (Pyralidae) |

The global distribution of *Diadegma* sp. is uncertain. *Diadegma* is a widespread genus, with representatives in all zoogeographical regions of the world (Gauld 1984). Therefore the possibility that this species may be represented in Hawaii was explored. The recorded *Diadegma* species of Hawaii and New Zealand are shown in Table 4.3 (which does not include all of the several undescribed *Diadegma* species in New Zealand). *Diadegma* sp. from *A. ptyoptera* is not one of the three species of *Diadegma* known to be present in Hawaii (Beardsley pers. comm.). The available evidence suggests it is a New Zealand endemic; it does not match any known *Diadegma* species from Europe (Fritton pers. comm.), Australia (Naumann pers. comm.) or North America (Townes pers. comm.). Further, it is related to several undescribed New Zealand species (Townes pers. comm.) and attacks a New Zealand native.

Even if *Diadegma* sp. is restricted to New Zealand, it is possible that one of the Hawaiian *Diadegma* could 'adopt' *A. ptyoptera*. Although Ichneumonidae constitute 20 percent of all parasitic insects (DeBach 1974), they are the least evolved parasites and hence not specialised to one host. As a result, ichneumonids tend not to be host specific but 'specific to certain situations, e.g., borers of various species...' (Townes 1971). However, the habitat ranges of the Hawaiian *Diadegma* spp. (i.e., mainly *Brassica* and *Solanum* spp. (Spiller & Wise 1982)) do not appear to include gorse. Therefore the chances of the Hawaiian *Diadegma* adopting *A. ptyoptera* are considered slim.

The effect of other parasites in Hawaii, however, cannot be predicted. Howarth (1983) reported that biocontrol by Lepidopterous herbivores in Hawaii is now difficult due to the introduction of many generalist parasitic Hymenoptera. For this reason, the parasitology of other gorse control Lepidoptera in Hawaii (see Section 2.3.6) should be monitored.

The two rearing enclosures used to estimate the percentage parasitism were the battery jars and perspex incubators. Because longer stems could be enclosed in the perspex incubators, these maintained the condition of the culture longer and were deemed the superior technique for achieving specimens and therefore gave better results (see Section 5.4).

Estimates of parasitoid impact per host generation are strongly influenced by host and parasitoid phenologies, and hence the method of sampling and calculation are critical (Kiritani & Dempster 1973; Southwood 1978). Van Driesche (1983) suggested that there are four ecological processes that need to be considered when determining percent parasitism. These are the extent and timing of: i) hosts entering (HI) and ii) leaving (HO) the susceptible stage; iii) parasitoid oviposition (PI); and iv) the emergence of adult parasites (PO). The degree of overlap of these process is also an important variable.

Because parasitised larvae and pupa could not be differentiated from non-parasitised, and because field sampling was by necessity destructive, it was necessary to use enclosure techniques where the hosts (unparasitised) and parasites that emerged (HO, PO) could be recorded. By dissection of the branches when HO & PO were complete, this method also enabled the number of hosts and parasites that had entered the system (HI, PI) to be measured.

Despite the overlapping generations of *A. ptyoptera*, the collection of the branches was timed so the parasitism of a single generation would be expressed, i.e., the generation about to emerge. However, because of uncertainty regarding both the host's and the parasitoid's phenologies as well as the host stage(s) susceptible to parasitism, this sampling technique could possibly have resulted in sampling the parasitism of two generations, although this is unlikely. Because parasite oviposition is most likely to have occurred on early instars, it is hoped that hosts were not removed before parasitism was complete.

The results of the stem dissections are shown in Table 4.4. From these results two things are immediately apparent: i) the level of parasitism appears high; and ii) the results from the two sites are remarkably similar. As only one replicate was taken from each site, no statistical test of significance with regards to the difference between the sites is possible. A single mean value from both sites was not used because parasitism is unlikely to be spatio-temporally stable, hence summing across time or between sites is of little value and unclear meaning (Van Driesche 1983).

**TABLE 4.4: Percent parasitism data: the number of *A. ptyoptera* larvae and pupae recovered and parasitoids reared from gorse branches from Greenpark and Burnham, MC.**

| BRANCH DISECTION DATA | Location: Burnham, MC | Greenpark, MC |
|---|---|---|
| Emerged Pupa | 17 | 16 |
| Unemerged Pupa | 4 | 2 |
| *Diadegma* sp. cocoons | 17 | 15 |
| *Zealachertus* sp. exuvia | 0 | 17 (2 hosts: 9 + 8) |
| Dead larvae | 13 | 9 |
| Live larvae | 0 | 0 |
| **PERCENT PARASITISM** | | |
| -all species | | |
| - including dead larvae | 33.3% | 38.6% |
| - without dead larvae | 44.7% | 48.6% |
| -*Diadegma* sp. | | |
| - including dead larvae | 33.3% | 34.1% |
| - without dead larvae | 44.7% | 42.9% |
| -*Zealachertus* sp. | | |
| - including dead larvae | - | 4.5% |
| - without dead larvae | - | 5.7% |

Because the number of hosts and parasitoid puparia could be counted with the technique used, it was possible to use the formula:

$$\text{Percent Parasitism} = \frac{\text{All emerged parasites}}{\text{All hosts (parasitised \& unparasitised)}}$$

However, the actual percent parasitism is unclear because it is unknown how many, if any, of the dead larvae were parasitised (i.e., they do not clearly fall into PO or HO). As dead or moribund larvae were found in the field very infrequently, the high rate of larval mortality is probably due to some aspect of the rearing technique; this is almost certainly the deterioration of the gorse stems.

Table 4.4 shows that the inclusion of the dead larvae in the calculation makes a dramatic difference to the percent parasitism result. In all probability, some but not all of the dead larvae were parasitised. Therefore it is concluded that the percent parasitism for the observed *A. ptyoptera* populations in the 1987 season was between 33.3 and 48.6 percent; comprising 33.3-44.7 percent by *Diadegma* sp. and 0-5.7 percent by *Zealachertus* sp.

The effect of parasitism was not assessed. However, its influence is likely to be expressed in many aspects of the biology of *A. ptyoptera*, including population dynamics (Doutt 1959), development rate (Nealis 1987) and instar progression (see Section 3.2).

Although the results in Table 4.4 suggest otherwise, the level of parasitism was found to vary between locations. For example, the Taitapu site was observed to have lower levels of parasitism than Burnham over the course of the weekly field monitoring exercise. In addition, the level of parasitism was found to change between seasons. The number of *Zealachertus* sp. observed at Burnham site increased in the 1988/89 summer (compared with 1987/88) while the number of *Diadegma* sp. declined.

Because the level of parasitism was monitored over only one season, the long term impact cannot be assumed (Van Driesche 1983). However, given the likelihood that parasitism is not stable, it is possible that periodic high levels of parasitism do cause local *A. ptyoptera* population crashes as Butler (1979) suspected (but did not observe). However, although the regrowth of gorse was noted, no *A. ptyoptera* population crashes were observed during this study.

**Other mortality agents**

Occasionally, larval carcasses were found with fungal fruiting bodies. It is unknown if these fungi were pathogenic or saprophytic; there is a proposal to examine this issue over the 1990/91 season (Hill pers. comm.). If pathogenic fungi do attack *A. ptyoptera*, this represents a quarantine consideration. Further, the occurrence of pathogenic diseases may indicate susceptibility to generalist diseases in the place(s) of introduction. However, mortality from this cause is probably less than five percent of the larvae.

A mortality agent that was noted but not investigated was spider predation of *A. ptyoptera* adults. The impact of spider predation is quite possibly considerable (Riechert 1974; Nuessly & Goeden 1983), as the spider population in gorse in summer appears to be large. The quantification of spider predation is possible (see Sunderland 1988) and this aspect may warrant further investigation.

### 4.4.4 Sub-Section Summary

Parasitoid attack on weed biocontrol agents in the place of introduction probably hinders establishment, and almost certainly limits effectiveness.

No egg or pupal parasitism of *A. ptyoptera* was found, although there is limited evidence that suggests egg parasitoids do exist.

The larvae of *A. ptyoptera* were found to suffer a high rate of parasitism. *Diadegma* sp. is a solitary ichneumonid that parasitised between 33.3 and 44.7 percent of the larvae. *Zealachertus* sp. is a gregarious eulophid that parasitised between 0 and 5.7 percent of the larvae in the samples.

*Zealachertus* sp. is restricted to New Zealand. The endemicity of *Diadegma* sp. is not certain but it is thought also to be a New Zealand species.

The immature stages of *A. ptyoptera* do not appear to be much affected by generalist mortality agents. However, adult mortality due to spider predation in gorse may be significant.

## 4.5 Fecundity and Fertility

### 4.5.1 Introduction

A fundamental component of any organism's demography is its reproductive potential. Reproductive potential is a function of many things, including: fecundity, fertility, body size, number of generations per year (voltinism), age at first breeding, etc. (Krebs 1978). The symbol "r" is commonly used to denote the reproductive potential of an organism. This section addresses the issues of fecundity and fertility. Other aspects of r have been discussed in section 4.2 (adult size & voltinism). Fecundity is a measure of total egg production per female, and fertility is the number or percent of viable eggs laid (Krebs 1978; Southwood 1978). Natality may be considered as a function of fecundity and fertility (Ashby 1972).

There are two methods generally recognised by which fecundity is measured. The potential fecundity may be measured by counting the eggs in pupae or newly emerged females. For insects where all the eggs are mature on emergence (pro-ovigenic - *sensu* Flanders 1950), this method may over-estimate field fecundity. For insects in which ovigenesis is not complete at emergence but more or less continuous thereafter (synovigenic), this method would give an under-estimate.

The other method of assessing fecundity is to measure actual fecundity, i.e., count the number of eggs laid by caged females. This method is used for synovigenic insects (Southwood 1978), but usually under-estimates field fecundity.

Ashby (1972) reviewed several methods used to correct estimates of fecundity derived from the above methods. He concluded that it is difficult to relate measured fecundity to actual field fecundity because of the interaction of many factors.

The examination of past weed biocontrol projects (Crawley 1986, 1987, 1989a) suggests that features associated with high rates of increase (high fecundity, small body size, short generation time etc.) are positively correlated with the likelihood of establishment. A theoretical explanation of this result is that the rapid growth of small founder populations would reduce the risk of local extinction (Gaston & Lawton 1988). Insects with high reproductive potential also appear to have a greater effect on the target (Crawley 1986), although it is unclear why this is so (Lawton in press). The importance of reproductive potential in weed biocontrol agents is reflected in the scoring systems of Harris (1973) and Goeden (1983).

### 4.5.2 Materials and Methods

Fecundity was examined over the summer of 1987/1988. Adults were obtained both by rearing pupae that had been recovered from samples of gorse taken in the weekly field monitoring and other field collections, and from the perspex incubators described in Section 4.4.

FIG. 4.18: Small cage placed over a small potted gorse bush as used to test the fecundity and fertility of *A. ptyoptera*

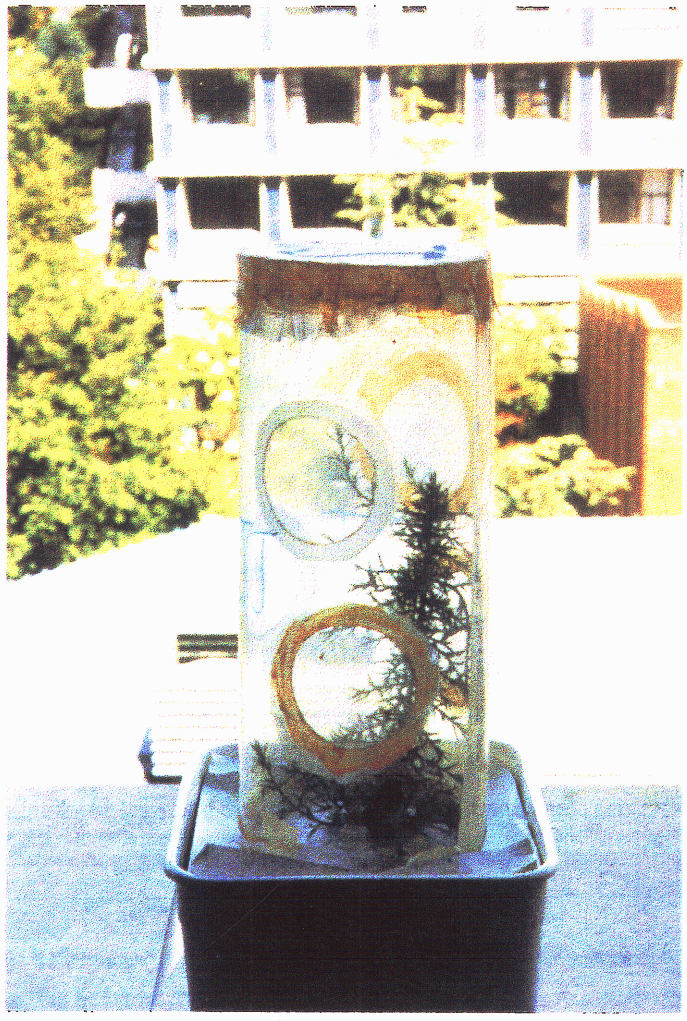
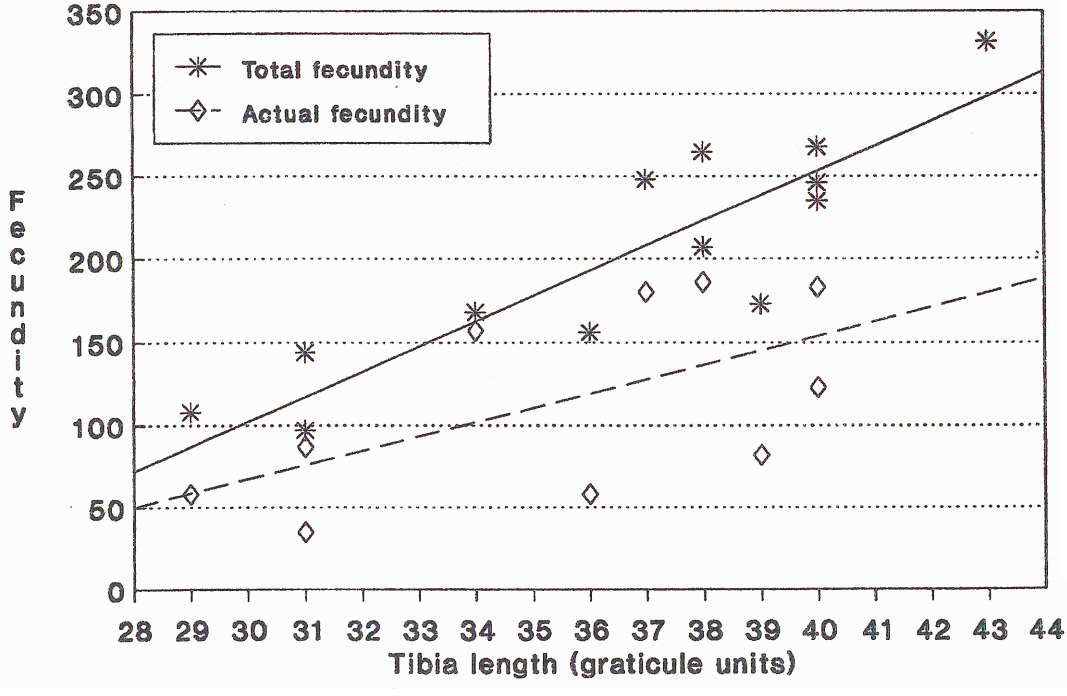


FIG 4.19: *A. ptyoptera* female tibia length versus total and actual fecundity



Actual fecundity was obtained by caging a pair of moths in a 295 mm high x 120 mm diameter cylindrical perspex tube with six 60 mm ports. The ports and one end of the tube were covered with nylon gauze. The cage was placed over a small potted gorse plant and sealed to a piece of cardboard that covered the soil at the top of the pot (see Fig. 4.18). A cotton wool dental roll soaked in a honey and water solution was placed in the bottom of the cage and replaced every other day. The pairs consisted of a male and a virgin female. Because delays in mating negatively influence the fecundity of females, all efforts were made to standardise the introduction of the male to one day or less after the emergence of the female. However, occasionally it was necessary to delay mating because of non-availability of males.

The cages were kept at room temperature (mean approximately 20$^{o}$C range: 14-30) and natural light regime - although direct exposure to the sun occurred only after 3 p.m. Attempts were made to standardise the temperature by using constant temperature cabinets, but because of a fatal malfunction, the use of constant temperature cabinets was abandoned.

The cages were inspected daily. When the female had died, the cage was removed and the female kept for later measurement and dissection. After 14 days, both the cage and its contents were examined for eggs and the number of eggs laid recorded. Because the number of *A. ptyoptera* adults was limited, potential fecundity could not be measured by dissection of recently emerged females. As a compromise, the "total" fecundity was measured by dissecting the females used in the actual fecundity experiments shortly after death and counting the number of eggs in the ovaries. The total fecundity was achieved by adding the actual fecundity to the number of eggs found in each dissected female.

Fertility was measured as a percent of the number of eggs laid in the cylindrical cages. As the time from oviposition to eclosion is five to seven days, the eggs were left for 14 days to allow ample time for any late emergences. Unemerged eggs are easily distinguished under a hand lens and were recorded separately during the egg counts. Fertility is expressed as the percent of fertile (emerged) eggs in the actual fecundity.

### 4.5.3 Results and Discussion

Females generally commenced oviposition within three to four days of introduction to the plant material. The fecundity and fertility data are shown in Table 4.5, along with age of the females (in days) at mating and longevity. It is immediately noticeable that there is significant variation in both the total and actual fecundity.

From the various exercises undertaken to rear *A. ptyoptera* adults, it appears that the sex ratio is 50:50. From these exercises, it also became apparent that there were two sizes of adult.

**TABLE 4.5: Fecundity and fertility performance of female *A. ptyoptera* in small arenas at room temperature.**

| Female | Size | Age at mating | Longevity | % Fertility | Fecundity | | |
|---|---|---|---|---|---|---|---|
| | | | | | Actual | Dissected | Total |
| A | L | 1 (d) | 18 (d) | 86.2% | 58 | 98 | 156 |
| B | L | 3 | | 81.2% | 186 | 21 | 207 |
| C | L | 4 | 22 | 79.7% | 123 | 145 | 268 |
| D | L | 1 | 1 | Female died | - | 235 | 235 |
| E | S | 1 | | Spider ate female | - | - | - |
| F | S | 2 | 12 | 77.1% | 35 | 109 | 144 |
| G | L | 1 | 6 | Female died | - | 332 | 332 |
| H | L | 1 | 2 | 80.3% | 183 | 63 | 246 |
| I | S | 1 | 2 | Female died | - | 97 | 97 |
| J | L | 1 | 6 | Female died | - | 265 | 265 |
| K | - | 1 | 10 | Spider ate female | - | - | - |
| L | S | 1 | 17 | 82.8% | 157 | 11 | 168 |
| M | S | 1 | 15 | Spider ate female | - | - | - |
| N | S | 1 | 7 | 89.6% | 87 | 10 | 97 |
| O | L | 1 | 20 | 98.3% | 180 | 68 | 248 |
| P | - | 1 | 15 | Spider ate female | 123 | - | - |
| Q | S | 3 | 16 | 70.7% | 58 | 50 | 108 |
| R | L | 17 | 27 | 73.6% | 82 | 91 | 173 |

Upon further investigation, a positive correlation was found between the size of the females and fecundity (See Fig. 4.19 - for total fecundity, $r = 0.8903$; $dof = 12$; $p = 0.05$). This phenomenon has been found in a wide range of insects (see references in Southwood 1978), including other gelechiids (Briese 1986). Because *A. ptyoptera* adults have two distinct size classes (see Sections 3.2 & 4.2), the effect of size on fecundity is considerable. The influence of size was also manifested in all other aspects of the reproductive potential examined. Therefore it was considered more accurate to divide the sample population into its respective size categories (large and small - taking the tibia length of 35.5 graticule units as the point of division) and examine each size class separately (see Table 4.6).

The mean total fecundity for the large females is 236.3. This is almost twice the small females' mean total fecundity of 122.8. This large difference in fecundity indicates the reduced reproductive potential experienced by the small adults.

Average fertility was 82 percent. There did not appear to be any difference between the two size classes (tested using a Mann-Whitney non-parametric test). However, the age of the female at mating did affect the fertility (see below).

**TABLE 4.6: Total and actual fecundity results from *A. ptyoptera* adults divided into large and small size classes.**

| | n | $\bar{x}$ | s | S.E. | Range |
|---|---|---|---|---|---|
| **Large** | | | | | |
| -Actual | 6 | 135.3 | 56.23 | 23.96 | 58 - 186 |
| -Total | 9 | 236.3 | 52.86 | 17.62 | 156 - 322 |
| **Small** | | | | | |
| -Actual | 4 | 84.25 | 52.96 | 26.48 | 35 - 157 |
| -Total | 5 | 122.8 | 31.79 | 14.22 | 97 - 168 |
| **Total** | | | | | |
| -Actual | 11 | 115.64 | 55.27 | 16.8 | 35 - 186 |
| -Total | 14 | 196 | 72.46 | 19.36 | 97 - 332 |

In all cases, the actual fecundity was less than the total fecundity. A comparison of the mean values for actual and total fecundity showed the large females laid 57 percent of their eggs, and the females in the small size class laid 69 percent. However, the standard errors of the means suggest that these values may be unreliable, although this difference between large and small is also expressed in the divergence of the regression lines for actual and total fecundity in Fig. 4.19.

It is unknown if *A. ptyoptera* is a pro- or synovigenic species. The total fecundity of females D, G, I & J, which did not lay and died shortly after emergence, is, in general, considerably greater than the mean actual fecundity for their respective size classes. This suggests that *A. ptyoptera* is pro-ovigenic. However, the reduced fecundity in females where mating was delayed argues against this proposal.

The effect of delayed mating in Lepidoptera has been examined by Proshold *et al.* (1982) and in the gelechiid *Pectinophora gossypiella* (Saunders) by Lingren *et al.* (1988). It appears that delayed mating reduces fecundity and fertility and the number of matings, but increases longevity. Although delaying mating was not studied here, a Mann-Whitney U-test showed the smaller females that had delayed mating (B, C, F, Q, R) appear to have had significantly lower fecundity and fertility. In the larger females, there appeared to be a significant reduction of fertility in the delayed mating subset, but there was no significant difference between the fecundity of the delayed and non-delayed mating treatments.

However, the results from the above test are limited in reliability because there are so few samples in each set. The effects of delayed mating may warrant further investigation. Given the demonstrated influence of delayed mating in other Lepidoptera, it is assumed that it does affect the reproductive potential of at least some *A. ptyoptera* females. Therefore, in addition to the effect of size, the influence of delayed mating is superimposed on the results.

Other features of the laboratory environment almost certainly also influenced the reproductive behaviour of the moths, e.g., temperature, humidity and food (Chiang 1985). As these variables are dramatically different from field conditions, as is the confined space available to the moths, it is assumed that the above results are only an approximate estimate of the reproductive potential of *A. ptyoptera*.

### 4.5.4 Sub-Section Summary

There is a positive correlation between female size and fecundity. As there appear to be two adult size classes, aspects of the reproductive potential of each size class were calculated separately. The mean total fecundity for the large females was 236.3 and 122.8 for the small females. Average fertility was 82 percent; there did not appear to be any difference between the two size classes. The age of the female at mating influenced fertility but had a variable effect on fecundity. In all cases the actual fecundity was less than the total fecundity. The average total fecundity was 196 eggs . Insofar as biocontrol assessment goes, the reproductive potential of *A. ptyoptera* appears at least reasonable. When compared to the low fecundity of most gorse feeders (Hill 1982), the reproductive potential of *A. ptyoptera* is very good.

# *SECTION V: The Potential of A. ptyoptera as a Biocontrol Agent*

## 5.1 Section Introduction

Schroeder & Goeden (1986) reported that 'naturalised weeds are generally colonized by certain native and accidentally introduced insects, but these are usually of little value as biological control agents... .' This claim is questioned given that: i) there are examples of accidental introductions damaging exotic weeds. New Zealand examples include: *Leucoptera spartifoliella* Hübner (Lepidoptera: Lyonettidae) attacks *Cytisus scoparius* (Scheele & Syrett 1987), and *Eriophyes genistae* attacks gorse (Hill & Gourlay 1989); and ii) some "new associations" have provided successful control (Hokkanen & Pimentel 1984, 1989). Hokkanen & Pimentel 1989 have defined new associations as those in which the exploiter is from a different geographical region to the host (and possibly from a different host). The potential of *A. ptyoptera* as a biocontrol agent also contradicts the claim of Schroeder & Goeden (1986).

Using agents from geographic locations other than around the pest's evolutionary centre of origin is contrary to the conventional practice of searching for candidate agents (see Section 2.4.4.1). Biocontrol convention has been and is to select natural enemies that are preadapted to the target pest species (Laing & Hamai 1976; Clausen 1978). It is generally assumed that agents should be from the native area of the target species, preferably near its evolutionary centre of origin (Bartlett & van den Bosch 1964; Huffaker *et al.* 1971; Zwolfer *et al.* 1976). This assumption rests on the belief that, because of a long period of co-evolution at the evolutionary centre of origin of the target, this region will contain the greatest diversity of and the most specialised natural enemies, and the most specialised agents are assumed to be the most effective (DeBach 1964; Huffaker *et al.* 1971; Huffaker *et al.* 1976).

Pimentel (1963) and Hokkanen & Pimentel (1984) have argued the opposite, i.e., that enemy-victim associations co-evolve to become less damaging to the host. Hokkanen & Pimentel (1984) proposed that this relationship should be applied to biocontrol - because new associations have not reached a stable ecological homeostasis, they are more damaging to the host. Therefore, they suggested, new associations a have higher probability of providing successful control than those based on long-evolved associations. From this, Hokkanen & Pimentel recommended that new associations should be favoured when selecting biocontrol agents, especially for biocontrol of native pests (Hokkanen 1986). In addition, Hokkanen & Pimentel advocated that natural enemies of close relatives of the target should be selected.

This hypothesis is an extension of Pimentel's "genetic feedback" hypothesis (Pimentel 1961, 1968) and refers to both insect and weed biocontrol attempts. It is perhaps the most controversial generalisation to have been made in biocontrol. The analyses and findings of Hokkanen & Pimentel (1984) have attracted a storm of criticisms. These include: inaccuracies in the classification of new and old associations (Goeden & Koh 1986; Greathead 1986); a bias in the data towards cactaceous insects (Goeden & Kok 1986); the omission of cases in which agents failed to establish, and hence distortion of the results (Harris 1986 - cited

in Lawton in press); inclusion of examples where several enemies have been combined to achieve the result, as well as errors in classifying the degree of success (Greathead 1986); many cases where new associations have failed (Goeden & Kok 1986; Crawley 1989c); double counting of successful programmes (Waage & Greathead 1988); and the use of unnecessary, elaborate data manipulation which appears to create erroneous results (Lawton in press).

Further, using agents from a new association raises, by definition, the thorny issue of the agent being able to transfer to novel hosts. This issue is discussed in Section 5.4.

The notion of Hokkanen & Pimentel (1984) - that exploiter-victim relationships co-evolve to become more benign - has also been questioned. Uncertainties include the following.
i) Current theory does not support the concept (May & Anderson 1983; Waage & Greathead 1988). May & Anderson (1983) suggested that natural enemies becoming less harmful is only one of several possible outcomes in the co-evolution between parasites and hosts.
ii) There is no clear evidence from the field that the effectiveness of natural enemies has decreased during the course of classical biocontrol of insects pests (Boulétreau 1986) or weeds (Harris 1986; Goeden & Kok 1986).
iii) Laboratory experiments claimed to support Pimentel's (1963) theory are not convincing (Boulétreau 1986; Waage & Greathead 1988).

On the other hand, some biocontrol attempts that have used new associations have provided effective control (e.g., Drooz *et al.* 1977; Carl 1982; see Hokkanen & Pimentel 1989 for others), although because of the predominant use of old associations in biocontrol, there are relatively few new association test cases. Denhill & Moran (1989) examined the new association principle using herbivore-plant relationships affecting agriculture in South Africa. They supported the claim of Hokkanen (1986) that new associations offer a large pool of potential biocontrol agents, and concluded that new associations can be very damaging and are not necessarily unsafe with regard to host specificity. However, Denhill & Moran (1989), like Waage & Greathead (1988), advocated a balance of both old and new associations while pointing out that host specificity remains the most severe constraint on agent selection.

The relationship between gorse and *A. ptyoptera* conforms to the definition of a new association of Hokkanen & Pimentel (1984, 1989) in that the species originate from different geographical areas and any interaction between them is at the most 150 years old (Hill pers. comm.). As noted earlier, *A. ptyoptera* is thought to be the first New Zealand phytophagous insect given serious consideration as a biocontrol agent (Hill pers. comm.), and it is almost certainly the first to be considered as an agent for a weed exotic to New Zealand (Hill unpub.). Regardless of the accuracy of these suppositions, if the *A. ptyoptera* programme proceeds, it will provide valuable empirical evidence for the use of the New Zealand fauna as a biocontrol resource and for the new association approach.

In this section, some aspects used in evaluating the potential of biocontrol candidates are examined. The evaluation systems of Harris (1973) and Goeden (1983) are based on a three tiered system of assessment. The first tier is an initial assessment of potential effectiveness. Many of the aspects within this tier have been discussed in Section IV and another is discussed in Section 5.2 (The Damage Characteristics of *A. ptyoptera*). The second and third tiers are "the suitability of the candidate as a biocontrol agent" and "its potential effectiveness in the proposed area of introduction" respectively. The criteria within the second tier are considered in Section 5.3 (culturability) and 5.4 (host range and possible host specificity screening techniques). Although the ecoclimatic similarity of the native range of *A. ptyoptera* and possible areas of introduction are not discussed, the distribution of the moth in New Zealand is examined (Section 5.5).

## 5.2 The Damage Characteristics of *A. ptyoptera*

### 5.2.1 Introduction

There is a large body of literature that relates reduced plant performance to the quantity of defoliation by insects (see Kulman 1971 and references therein; Crawley 1989a). However, references that concern damage by weed biocontrol agents are rare.

There are several facets that might be considered when assessing damage. According to the scoring systems of Harris (1973) and Goeden (1983), the type and timing of the damage caused by a weed biocontrol candidate are primary considerations. The timing of damage is considered in relation to the phenology of the target. As outlined in Section 2.4, agents that damage the weed at the most critical phase in its phenology and/or over a prolonged period are desirable.

The type of damage inflicted by weed biocontrol agents has traditionally been evaluated by the plant structures that are attacked. Recently the relationship between the plant parts that a weed biocontrol agent attacks and its effectiveness has been questioned (see Section 2.4.2 & 4.3).

Nevertheless, the type of damage inflicted by a weed biocontrol candidate is important information, and therefore, along with other parameters of damage, it is considered in this part of the study. Harris (1984) proposed that agents could be rated by the amount of annual production they remove or destroy, whereas Crawley (1989a) stressed the need for information regarding the agent's impact on the population dynamics of the target. Both of the above proposals are beyond the aspirations of this study, in which only the damage inflicted has been reported - not the effect of the damage. As a result, reliable value judgements cannot be made.

The aspects of damage considered in this section are: the timing and type of damage; the amount of foliage lost to *A. ptyoptera*; the relationship between plant age and damage, including when plants are first attacked (a component of an agent's virulence); the relationship between plant age and the oldest growth stage attacked; the relationship between growth stage attacked and the amount of foliage damage; and the amount of foliage damaged over one *A. ptyoptera* generation.

### 5.2.2 Materials and Methods

In order to assess the damage caused by *A. ptyoptera* feeding, three trials using separate plots were undertaken. The plots were at the Burnham and Taitapu field sites, described in Section 4.2 and another Burnham site that was similar to the first except that it had plants only two growth seasons old (i.e., having G0, G1, G2). At each site, 50 plants were selected by choosing every second plant occurring on a randomly selected 2 x 500 m strip. One randomly selected shoot was labeled and numbered on each plant.

The damage status of the shoot and the branch to which the shoot was attached was recorded, as was the amount of damage in each bush. Shoots were classified as green, yellowing or dead. If the branch was damaged, the site of larval feeding and the proportion of shoots affected by the damage was recorded. The damage status of the bushes was classified by recording the number of yellowing and the number of dead branches and the total number of branches. However, because branches are not of equal size, the percent damage suffered by each bush was also estimated. This was done by visualising each bush as a hemisphere divided into 20 segments of 18° each (i.e., each segment worth five percent). Then, by summing the affected segments and parts of segments, an estimate was made of the percent yellowing, dead and total damage.

In order to examine the correlation between plant age and damage suffered, the age of each bush at the beginning of the survey was recorded. The damage occurring in one *A. ptyoptera* generation was measured by reassessing the damage status of each shoot, branch and plant after 12 months. It was intended that the tagged shoot damage trial would:

i) give the amount of damage at each site;

ii) allow a comparison of the damage at climatically variable sites (Taitapu and Burnham) and a comparison between "mature" and "young" gorse plants;

iii) allow plant age to be correlated against the extent of damage;

iv) determine if older plants are attacked in older tissue;

v) enable the extent of foliage damage to be correlated against the growth stage attacked; and

vi) give the damage inflicted by one *A. ptyoptera* generation.

Because it was found that yellowing foliage inevitably died, the percentages of yellowing and dead foliage were pooled and the "total foliage damage" used in the analyses.

### 5.2.3 Result and Discussion

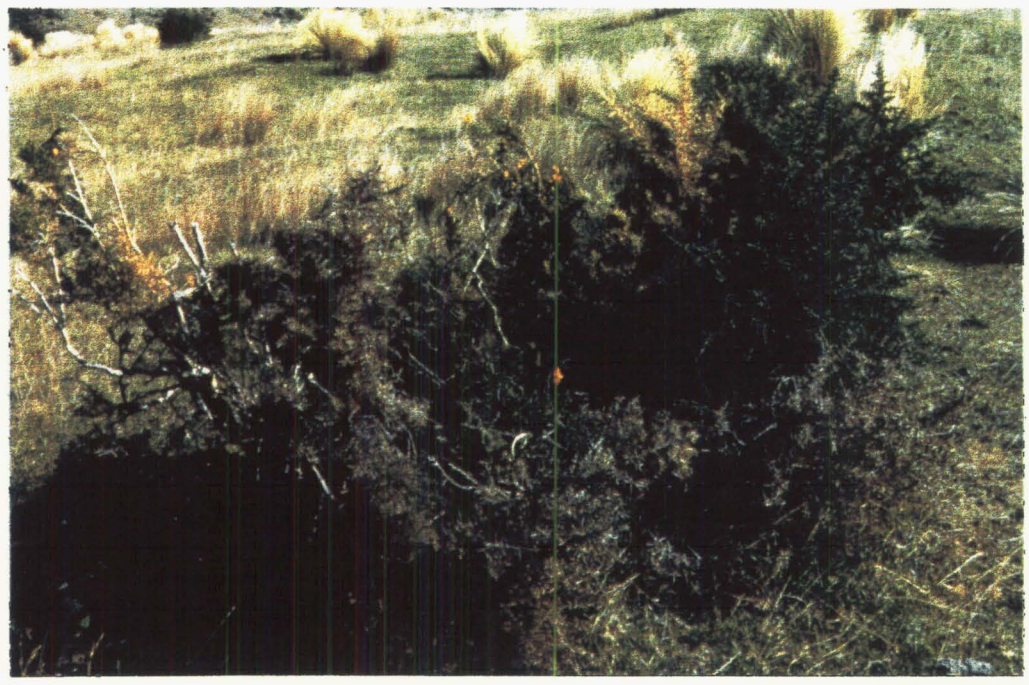
As discussed in Section 4.3, *A. ptyoptera* larval feeding disrupts vascular transport and structurally weakens the host. Vascular disruption often causes branches to yellow and eventually die-back (see Fig. 5.1). Occasionally *A. ptyoptera* damage contributes to the death of entire plants (see Fig. 5.2).

As outlined in Section 2.4, a prolonged attack period is a desirable attribute of a biocontrol candidate. Because of the unstructured life history of *A. ptyoptera* (see Sections 3.2 and 4.2), larval feeding occurs at all times of the year (see Fig. 4.6). As a result, damage to gorse continues throughout the phenology of the plant, affecting both its growth and flowering potential. (Gorse phenology at the study sites is shown in Fig. 2.1.)

Quantifying the effect of *A. ptyoptera* damage on the growth and flowering of gorse was beyond the means of this study. However, casual observations were made on these areas of plant performance. *A. ptyoptera* feeding does not always kill the branch in which it occurs (at least, not over the period of field observation),

**FIG. 5.1: Yellowing and die-back on a gorse bush due to *A. ptyoptera* attack. Burnham Feb 1985. Photograph courtesy of DSIR Plant Protection**

**FIG. 5.2: *A. ptyoptera* damage occasionally contributes the death of entire gorse plants. This plant has 85 percent foliage loss and subsequently died. However, note the regrowth. Taitapu MC, December 1987.**



but it usually does. Insect attack is often the cause of reduced plant growth rate (Heichel & Turner 1984; Kappel & Proctor 1986 - cited in Crawley 1989a), and not surprisingly, branches suffering *A. ptyoptera* feeding showed far less G0 elongation. Generally, branches that were yellowing made little or no G0 elongation, and all the marked yellowing branches died within 12 months. Although it was found that bushes could compensate for *A. ptyoptera* attack by regrowth (see Fig 5.2), the sections of branch above the feeding sites were never found to recover.

Although *A. ptyoptera* damage is most obvious around the end of flowering (because of discolouration and death of foliage), branches suffering *A. ptyoptera* feeding were judged to have fewer flowers and buds than non-attacked branches. However, possibly in an effort to compensate, attacked branches were sometimes found to have a prolonged period of flowering. The literature supporting the indirect effect of insect attack on flowering and fruit production has been recently reviewed by Crawley (1989a). Although no references were found concerning stem mining, it is assumed that *A. ptyoptera* attack has at least some impact on the reproductive potential of gorse.

Unlike flowering or growth, foliage damage could be quantified. The parameters of foliage damage are considered in the remainder of the section.

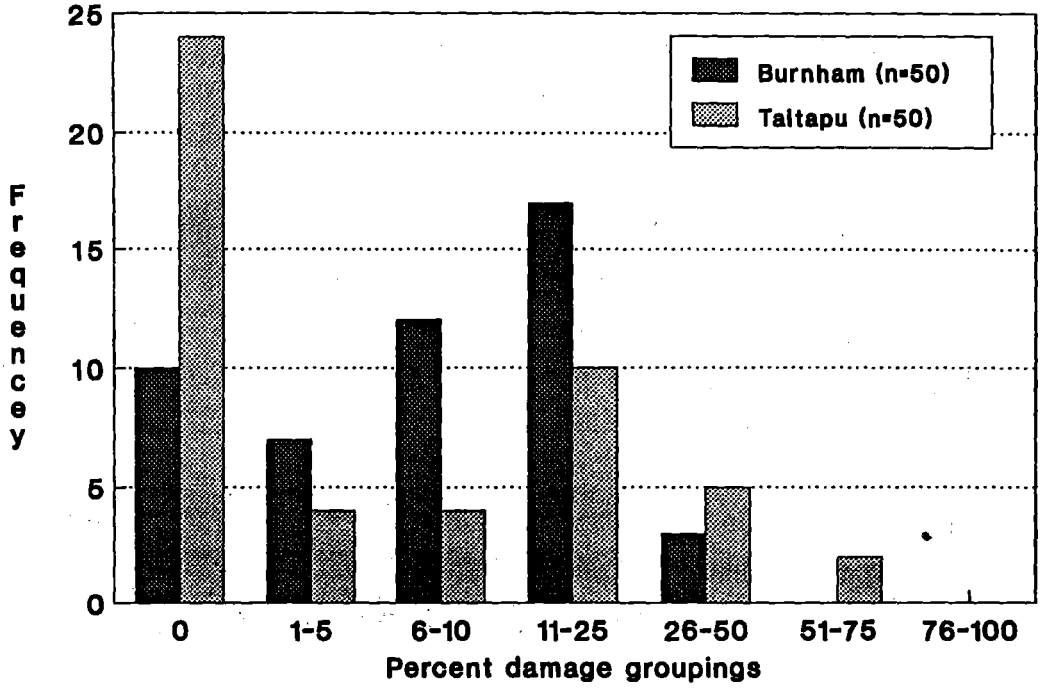
None of the plants at the second Burnham site (young plants) were attacked. Therefore the damage trial at this site was discontinued.

The initial part of the damage assessment was to quantify how much green foliage is lost to *A. ptyoptera* attack. This was examined by two approaches: i) by the examination of the individual marked shoots; and ii) by the visual estimation of percent foliage damaged.

At Burnham, the first approach indicated that 14 percent of the shoots were damaged. If one assumes all shoots are of equal size, it can be deduced that 14 percent of gorse foliage is lost to *A. ptyoptera* attack. This result closely agrees with the results of the second approach, where the mean estimated damage was 11.4 percent. At Taitapu, the two approaches also gave similar results; 10 percent of the shoots were damaged, and the visually estimated mean damage was 11.74 percent. From this it appears that both sites suffer a similar amount of total damage.

However, a closer examination of findings from the second approach (see Fig. 5.3) shows the two sites have quite different damage characteristics. At Taitapu at the beginning of the survey, 48 percent of the plants were not attacked. Of the plants that were damaged, the mean foliage damage was 22.6 percent and a few plants had considerable foliage damage (see also Fig. 5.4b). Conversely, 80 percent of the gorse plants at Burnham suffered some damage, but none of them had heavy foliage damage; of the Burnham plants attacked, the mean damage was only 14 percent.

FIG. 5.3: Total percent damage by *A. ptyoptera* on 50 marked gorse bushes at Burnham and Taitapu, MC. Nov 1987



However, as noted earlier, due mainly to differences in the age and history of the plants, direct comparison of the sites maybe misleading. As will be seen in the following discussion, foliage loss can be influenced by the plant age, thus the effect of age will be superimposed on any possible differences between the sites.

The lack of *A. ptyoptera* damage at the second Burnham site (with young plants) agrees with a theme observed at the other two sites; plants that are two seasons old or less are seldom attacked. However, the age at which plants are first get attacked is different at the two sites.

Figures 5.4a & b show the age of the plants versus the amount of foliage damaged at Burnham and Taitapu respectively. Fig 5.4a shows that two year old plants at Burnham suffered some attack, although the extent of foliage damage was small. On the other hand, at Taitapu two year old plants were not attacked and plants three years old generally suffered less damage than two year old plants at Burnham, with the majority suffering no damage at all.

As seen in Fig. 4.3a,b & c, the only notable climatic difference between the sites was the amount of wind experienced - Taitapu was on average, 26 times windier than Burnham. This suggests that the degree of exposure may contribute to the virulence of *A. ptyoptera*. As suggested in Section 4.3, windy conditions may limit the dispersal of adult moths and hence lead to an aggregation of the larval population and occasional intense damage as a result (as was found at Taitapu).

As well as the age at which plants are first attacked, the relationship between the amount of foliage damage and plant age was examined. At both Burnham and Taitapu there appears to be a positive correlation between plant age and foliage damage (see Figures 5.4a & b).However, at the Burnham site this relationship is weak, as indicated by the following. i) The coefficient of determination ($r^2$) is only 0.1017, indicating that only 10 percent of the variation is accounted for (i.e., wide variation about the line); high variation indicates that other factors or influences are involved in the relationship. ii) The amount of damage suffered by three and four year old plants is not statistically different ($t = 0.031$, $dof = 38$, $p = 0.05$).

In contrast, the relationship between the amount of foliage damage and plant age at Taitapu is more robust. Two and three year old plants were generally not attacked, and there was a progressive increase in the amount of damage suffered in plants 3, 4, 5 and 6 years old. However, $r^2 = 0.4453$, which again indicates high variance and the possibility of other factors influencing the relationship.

The positive relationship between plant age and foliage lost at Taitapu suggests that *A. ptyoptera* damage, probably in combination with wind and stock, may facilitate old-age deterioration. Whole bushes occasionally died within one season, but more typically they appear to degenerate with time. It appears that *A. ptyoptera* damage breaks up the "dense thicket" growth form of gorse and hence makes it more vulnerable to stock and weather damage. The movement caused by wind and stock may damage the crown and allow water to enter, leading to the deterioration of the bush. Studies that have demonstrated a decrease

FIG. 5.4a: Gorse plant age versus foliage damage by *A. ptyoptera* at Burnham, MC. Nov 1987

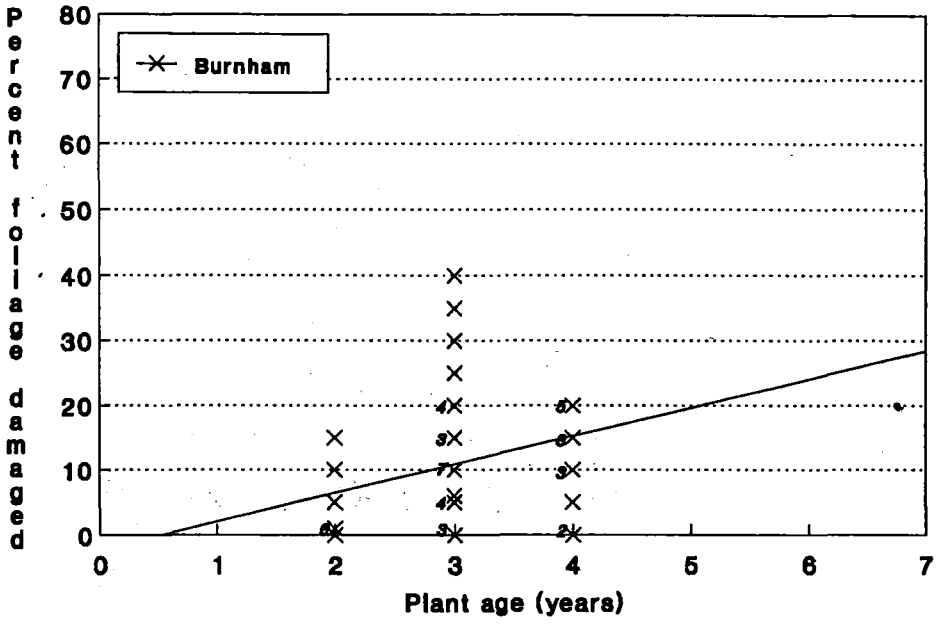
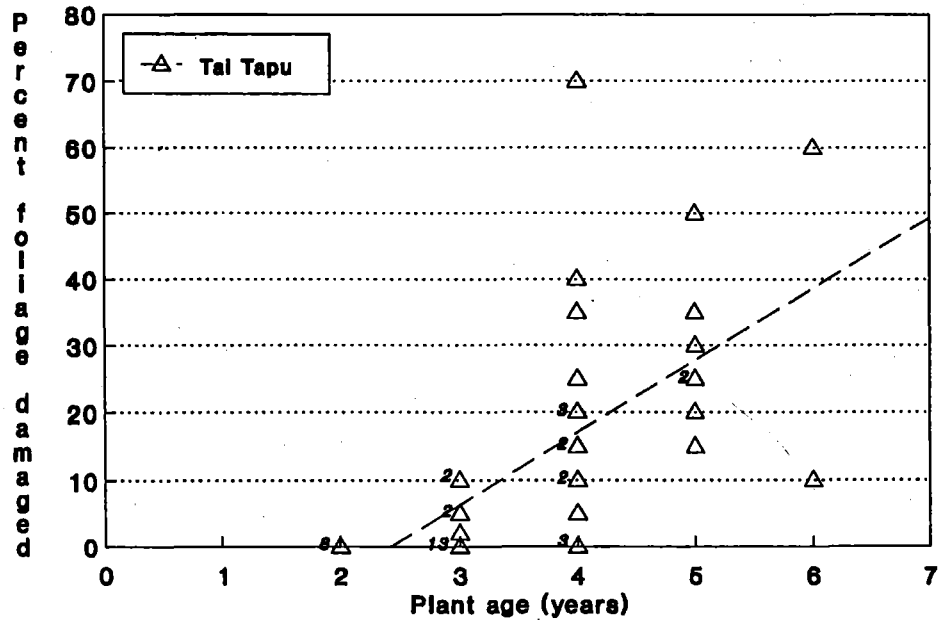



FIG. 5.4b: Gorse plant age versus foliage damage by *A. ptyoptera* at Taitapu, MC. Nov 1987



in plant longevity due to insect attack include: Waloff & Richards (1977) (a decrease in longevity of broom (*Cytisus scoparius*) due to the influence of several insect species) and Churchill *et al.* (1964), (a strong graded relationship between defoliation intensity of trembling aspen (*Populus tremuloides*) and longevity).

**TABLE 5.1: Student t-values from the relationship of gorse plant tissue attacked by *A. ptyoptera*, for each plant age group**

| Age of plants | t-value | dof | p |
|---|---|---|---|
| **BURNHAM** | | | |
| 2 v 3 | 3.88 | 34 | 0.05 |
| 3 v 4 | 1.82 | 37 | |
| **TAITAPU** | | | |
| 2 v 3 | 2.80 | 24 | 0.05 |
| 3 v 4 | 3.99 | 31 | |
| 4 v 5 | 1.89 | 20 | |
| 5 v 6 | 3.14 | 7 | |

Another relationship examined was plant age versus the oldest growth stage attacked. It was hoped that this examination would complement the larval location investigation of Section 4.3 and perhaps reveal if some of the relationship between age and damage maybe due to earlier wood being attacked in older plants. The relationship between plant age and the oldest growth stage attacked is depicted in Figures 5.5a & b. An examination of the data in Fig. 5.5a showed that at Burnham, the age of the oldest wood attacked increases with the age of the plants. Although three & four year old plants suffered similar patterns of attack, the mean age of the oldest tissue attacked is significantly older for each proceeding plant age (see t-values in Table 5.1). At Taitapu the oldest growth stage attacked also increased with plant age; the number of plants with no damage became progressively less as plant age increased and the mean age of oldest tissue attacked for each age class was significantly older than the previous age class (see t-values in Table 5.1).

The relationship between the growth stage attacked and the amount of foliage damaged was also examined. It was assumed that the older the tissue attacked, the greater the foliage loss would be. However, the data (shown in Figures 5.6a & b) do not support this hypothesis. A regression of the data in Fig. 5.6a revealed no correlation between the two variables at Burnham ($r = 0.21248$, $dof = 39$, $p = 0.05$). For the Taitapu study plants, there was a positive relationship ($r = 0.3873$, $dof = 26$, $p = 0.05$), but it was a very weak one. The large amount of variation around the line ($r^2 = 0.15$) casts further doubt on the credibility of this relationship.

An imprecision in the method used, however, means that the possibility of a relationship between growth stage attacked and amount of foliage damaged cannot be discounted. From the plant dissection experiments described in Section 4.3, it is known that the most common larval feeding site is G1 & G2. However, the information used to test the growth stage versus damage relationship does not include the

FIG. 5.5a: The age of gorse plant tissue attacked by *A. ptyoptera* for each plant age group at Burnham, MC. Nov 1987

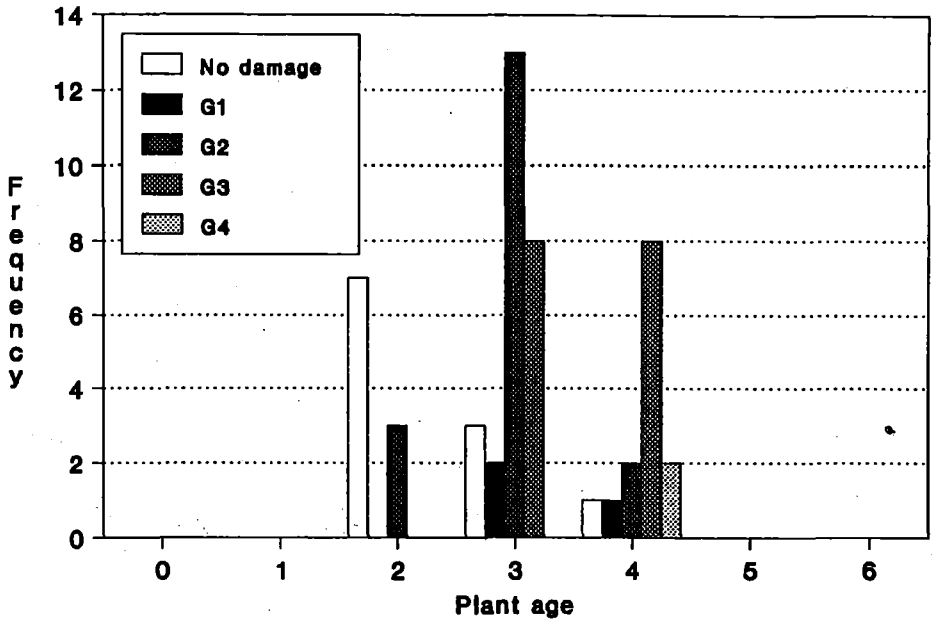



FIG. 5.5b: The age of gorse plant tissue attacked by *A. ptyoptera* for each plant age group at Taitapu, MC. Nov 1987

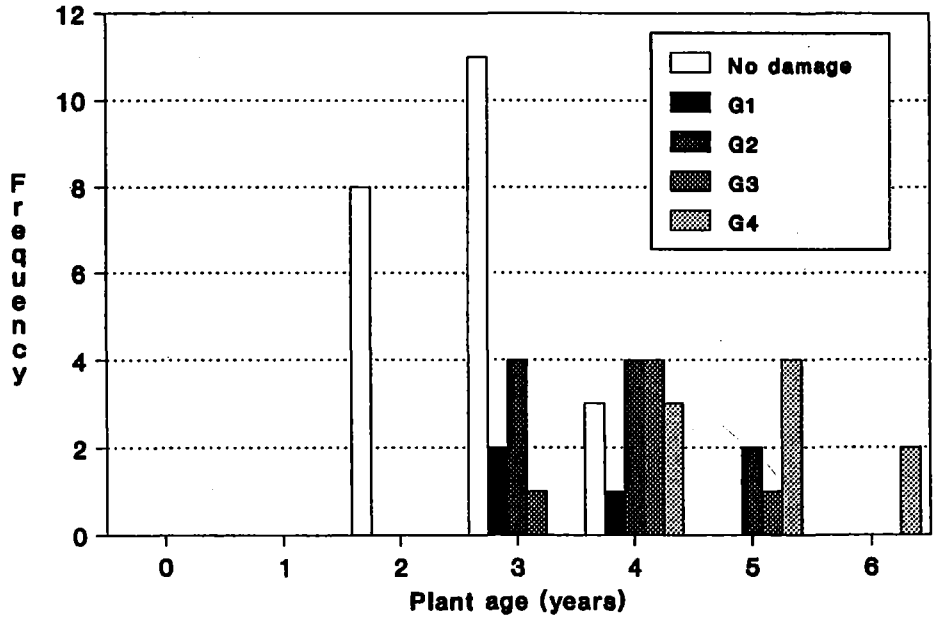


FIG. 5.6a: Growth stage of gorse plants attacked by *A. ptyoptera* versus the amount of foliage damaged. Burnham, MC. Nov 1987

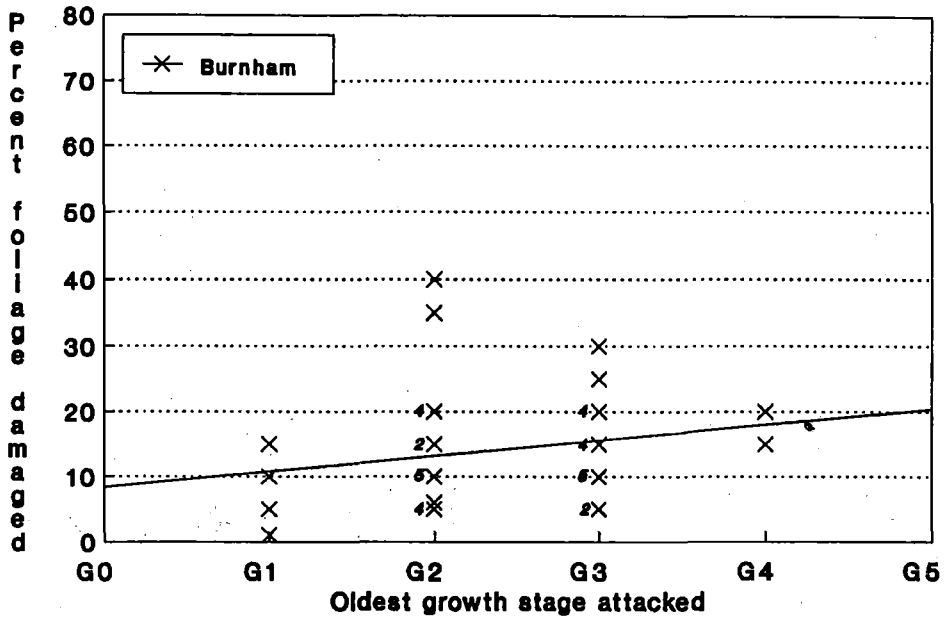
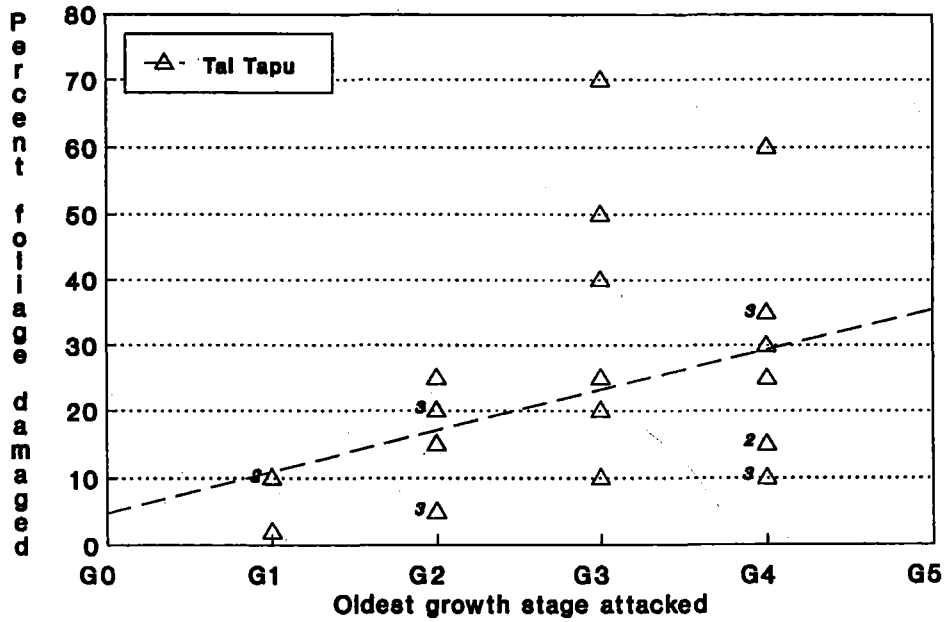



FIG. 5.6b: Growth stage of gorse plants attacked by *A. ptyoptera* versus the amount of foliage damaged. Taitapu, MC. Nov 1987



number of larva attacking the different tissues in each plant (and thus implies that the larvae are evenly distributed). In reality, the uneven distribution of the larvae probably disguises the relationship. For example, many larvae attacking young growth may produce visually similar damage to that of fewer larvae attacking older growth. Destructive sampling might have clarified the effect of larvae numbers on the growth stage versus damage relationship, but was not appropriate to this continuing study.
Fig. 5.7 shows the change in foliage damage over 12 months as an indicator of the amount of damage inflicted over one *A. ptyoptera* generation. As projected by the plant age versus damage relationship, an increase in the age of the study plants has, in most cases, led to an increase in the amount of foliage damaged. However, many plants had the same level of damage after 12 mouths (i.e., zero difference) and some plants had partially recovered (i.e., damage after was less than damage before). Also, perhaps not surprisingly, there is considerable variation between the two sites.

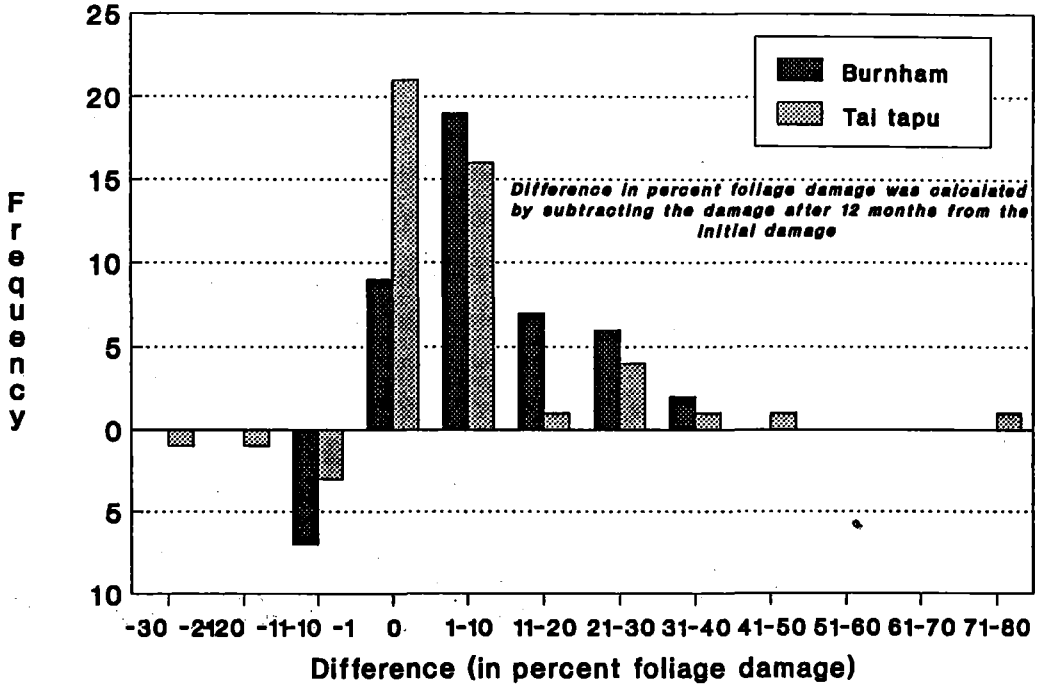
At Burnham, after 12 months, the mean change in damage according to the visual estimation was 7.8 percent (SE = 1.7). This is in relatively close agreement with the 12 percent mean increase derived by the tagged shoot exercise. Eighteen percent of the study plants had the same amount of damage and 14 percent had made some recovery. None of the study plants died and the maximum change was 40 percent. At Burnham, the maximum total damage at the end of this survey was estimated to be 50 percent.

At Taitapu, the visual approach estimated the mean increase in damage to be 6.64 percent (SE = 2.3). This is considerably less than the 14 percent mean increase indicated by the tagged shoot exercise. Although both approaches indicate an increase in foliage damage, given the tagged shoot approach cannot account for plant regrowth, I am inclined to have greater faith in the mean from the visual method.

Fig. 5.7 shows that 42 percent of the Taitapu study plants had no change in the amount of damage. (Note that this proportion is not the number of study plants that suffered no damage.) In agreement with the plant age versus foliage damaged relationship, as the age of the study plants increased by one year, the number of "no damage" plants was almost 50 percent less than at the beginning (14 verses 24).

Compared with Burnham, fewer of the Taitapu plants showed signs of recovery (10 percent), but two of these had considerable regrowth. Although the reason for the difference in recovery between the two sites is not known, it is known a plant's ability to regrow (and/or compensate) is dependent upon the timing of insect attack (Jackson & Scott 1980; Stamp 1984; Crawley 1989a) which maybe slightly different between the sites. Other environmental factors (e.g. soil quality etc.) may have also contributed. At the other end of the regrowth scale, one of the Taitapu study plants died (partially attributed to *A. ptyoptera* damage) which was recorded as 100 percent total damage.

FIG. 5.7: The change in foliage damage on 50 marked plants over one *A. ptyoptera* generation at two sites



### 5.2.4 Sub-Section Summary

Larval feeding by *A. ptyoptera* structurally weakens the host and disrupts vascular transport; this appears to reduce flowering and growth, causes die-back of branches, and occasionally contributes to plant death.

Several factors make the validity of the comparison between Burnham and Taitapu dubious. Nevertheless, it is proposed that differences in the damage characteristics at the two sites may be the result of habitat differences, specifically exposure to the wind and stock damage. The mean amount of total foliage damage was between 11.4 - 14 percent at Burnham and 10 - 11.74 percent at Taitapu. The amount of damage appears to be related to plant age and the degree of exposure of the plants, and possibly other variables. Predictably, the oldest growth stage attacked increased with plant age. However, at Burnham no relationship was found between oldest growth stage attacked and the amount of foliage damaged and at Taitapu this relationship was weak. Due to the imbalance in the amount of feeding in each growth stage (not accounted for in this work) it is unknown if this relationship exists or not. The study plants at both sites suffered an increase in the amount of foliage damaged over one *A. ptyoptera* generation. One plant was killed and many plants suffered one third defoliation or more. However some plants showed an ability to recover.

Given the regrowth and recruitment vigour of gorse, the damage measured is unlikely to "control" the plant. However, it appears *A. ptyoptera* reduces the growth and the reproductive potential and also facilitates old age deterioration and mortality. Therefore, *A. ptyoptera* is considered to have the potential to contribute to reducing the vigour of gorse growing outside New Zealand. *A. ptyoptera* may have a greater impact if it escapes colonisation by predators and parasites in a new country.

As an agent, *A. ptyoptera* is likely to be compatible with almost all other gorse biocontrol agents currently being used or considered in Hawaii, e.g. the seed feeder *Apion ulicis;* and the foliage feeders *Agonopterix ulicetella, Scythris gallicella* (Lepidoptera: Scythidae), *Tetranychus lintearius, Apion scutellare* (Coleoptera: Curculionidae), and *Sericothrips staphylinus* (Thysanoptera). Indeed, it may be possible, with a combination of the above agents, to achieve sufficient stress to be able to at least check the invassive progress of gorse. One possible gorse agent which *A. ptyoptera* may not be compatible with is *Chlorophorus trifasciatus* F. (Coleoptera: Cerambycidae). However, given the reported low degree of specificity of this agent (Zwolfer 1962), its use is uncertain.

## 5.3 Culturing *A. ptyoptera*

### 5.3.1 Introduction

As outlined in Section 2.4, the ease with which a candidate agent can be reared is one of the criteria by which it is judged. If a biocontrol candidate can be easily cultured, host specificity testing, quarantine and liberation procedures are greatly facilitated (Goeden 1983).

Insect rearing is central to most entomological endeavours, especially biological control (King & Morrison 1984). Since around the turn of the century, the science of insect rearing has developed parallel to modern entomology. It has become apparent that successful insect rearing is complex and requires an understanding of the insect's biology, including fecundity, longevity, and environmental and nutrition requirements (Singh 1984).

An important advance in rearing phytophagous insects was the development by Adkisson *et al.* (1960) of using wheatgerm as the primary nutrient source. Since then wheatgerm has been used in hundreds of insect diets (House *et al.* 1971; Singh 1977). An overview of dietetics and nutrition in insect diets is given in Singh (1984).

The literature concerning artificial diets for insects is large. Insect diets have been thoroughly catalogued by House (1967) and Singh (1977). Gomez (1978 - cited in Singh 1984) catalogued artificial diets for Lepidoptera. Most artificial diets appear to have been developed for entomophagous agents or phytophagous pests. Of the 19 references in Singh (1977) referring to Gelechiidae, all concern the pest species *Anarsia lineatella* Zeller; *Pectinophora gossypiella*; *Phthorimaea operculella* (Zeller); and *Sitotroga cerealella* (Olivier). In an incomplete search of the literature, no references were found on rearing stem-miners for weed biocontrol.

### 5.3.2 Materials and Methods

Over the course of this study, several techniques were used in attempts to obtain adults. The most primitive and labour intensive technique used was the collection of pupae and pre-pupal larvae from infested gorse bushes in the field. As described in Section 4.4, this method involved finding larvae and pupae in gorse, tying the covering bark back over the gallery, collecting the section of wood, and then maintaining the sections of wood in stoppered 10 x 25 mm cylindrical vials until the adult emerged.

A less laborious method of obtaining adults was to collect infested sticks without examining their contents, and place them in containers in the laboratory. In section 4.4, two methods of containment were described. These were: i) placing 250-300 mm sections of branches in battery jars (Fig. 4.14); and ii) placing whole branches (up to 900 mm long) in perspex incubators (Fig. 4.15). A third method of containing infested sticks was used in an attempt to delay the deterioration of the sticks that was encountered in i) and ii). In

this method, the branches were de-spined and stood in the 250 ml volumetric flask containing a dilute sucrose-critic acid solution (believed to prolong cut life (Salinger 1985)). The neck of the flask was then stopped with cotton wool and a 550 x 900 mm plastic bag was placed over the branch and sealed around the flask's neck. This arrangement was kept upright by clamping the flask and branch to a clamp stand.

Although using artificial diets to rear larvae was attempted primarily to examine the influence of photoperiod and temperature on the life history of *A. ptyoptera* (Section 4.2), the exercise has given valuable insight into rearing the agent. The methods used to rear field collected *A. ptyoptera* larvae on artificial diet have been outlined in Section 4.2.2. To reiterate: in October and November 1987, 20 mid-range instar larvae were introduced to general purpose diet (GPD) (Singh 1983) in lugless plastic petri dishes and subject to two different light regimes in controlled temperature cabinets. In August 1988, 41 larvae of various sizes were placed on GDP in 10 x 75 mm diet tubes and maintained at room temperature. The results from the 1988-89 diet trial are shown in Appendix Table III.2.

### 5.3.3 Results and Discussion

It is standard practice to ascertain the biology, behaviour, environmental and nutritional requirements, etc., of an insect before developing rearing techniques (Singh 1984), so attempting to culture *A. ptyoptera* in the preliminary studies may have been premature. However, information on a biocontrol candidate's ease of rearing is a very important practical consideration when evaluating that agent.

The collection of pupae and pre-pupal larvae was the most reliable means of achieving a given number of adults. However, because of the diffuse life history of *A. ptyoptera*, relatively few pupae or mature larvae were encountered in a day's searching, and collecting sufficient numbers is very wearisome and time consuming. In addition to the high labour requirement, field collection of immatures is necessarily destructive (making re-establishment of disturbed immature larvae difficult) and few individuals are obtained. Thus it is unlikely to be an appropriate method for rearing specimens for host specificity testing or liberation.

The other techniques that relied upon naturally reared larvae were the various stick containment methods. As noted in Section 4.4, the shorter sticks in the battery jars deteriorated more rapidly than the whole branches in the incubators. In addition, removing the adults from within the battery jars was very awkward and the specimens were often damaged in the process. Recovering specimens from the perspex incubators was not difficult and the whole branch cultures maintained themselves for four to eight weeks. However, because: i) many branches collected contain few or no larvae or pupae (i.e., low strike rate); and ii) the unsynchronised development of *A. ptyoptera* results in many specimens being unable to complete development before the branches die, relatively few adults were obtained despite considerable effort (e.g., on average 9.8 adults were obtained (range = 3-18) from each incubator. Gathering branches for one incubator takes one person one working day).

The clamp stand and volumetric flask method appeared to maintain the branches for a little longer. However, because each branch took so long to set up and produced few specimens, this technique is not recommended.

Because of the long development time (see Section 4.2) and stem boring habit in mature bushes of *A. ptyoptera* (see Sections 4.3 and 5.2), rearing this agent on plant material in quarantine without mature gorse plants will probably not be possible.

In addition to limitations caused by quarantine considerations, techniques that rely on field collections are labour intensive and unreliable. Therefore, culturing *A. ptyoptera* from neonate larvae on artificial diet is almost certainly the most appropriate technique for obtaining specimens for host specificity testing (especially outside New Zealand) and field release.

**TABLE 5.2: Summary of the results from the 1988-89 artificial diet trial**

| SIZE: | | Large | Medium | Small | Total |
|---|---|---|---|---|---|
| n: | | 14 | 19 | 8 | 41 |
| FATE: | Emerged | 50% | 31.6% | 25% | 36.6% |
| | Emerged deformed | 42 | 20 | 0 | 26.7 |
| | Failed to establish | 0 | 15.8 | 37.5 | 14.6 |
| | Death by dehydration | 14.3 | 10.5 | 12.5 | 12.2 |
| | Death by mould | 14.3 | 21.1 | 0 | 14.6 |
| | Parasitised | 7.1 | 10.5 | 12.5 | 9.8 |
| | Killed when handling | 14.3 | 10.5 | 12.5 | 12.2 |

The results from the attempts to rear *A. ptyoptera* on artificial diet were reported in Section 4.2.3. In summary, these results are: only two adults, both deformed, emerged from the 1987 petri dish culture. The results from the 1988-89 diet tube culture shown in Appendix Table III.2, are summarised in Table 5.2. It can be seen that using diet tubes and not using controlled temperature cabinets gave a better rate of success; of the 41 larvae in the 1988 culture, 15 adults emerged (four of them deformed). There appear to be positive correlations between the size of larvae introduced to the diet and the proportion that emerged, and between larval size and the rate of establishment.

The deformity mentioned above is thought to be due to either the wings of the adult not successfully disengaging from the pupal case before the wings harden, or a nutritional deficiency in the diet (see Chippendale *et al.* 1965).

The high rate of larval mortality was largely due to invasion of mould and diet dehydration. Contributing factors included: i) an inability to mimic the conditions inside a gallery (i.e., little or no free water but high

humidity) for 12 - 20 weeks; and ii) difficulties in striking and maintaining a balance in the diet between too much water (resulting in mould) and too little (dehydration).

However, with more sophisticated care of the environment in which the culture is held, the mortality could probably be reduced. For example, Anthon *et al.* (1971) successfully reared another internally feeding gelechiid, *Anarsia lineatella* Zeller, from neonate larvae on artificial diet, although the development time of this moth is considerably less than that of *A. ptyoptera*.

The results from the culturability trial contrasts with those of the field population, where larval death believed to be due to dehydration and fungal attack was only occasionally found. Combined with the high "failure to establish" rate, this suggests that the diet may have been unsuitable because of its high initial water content and its susceptibility to subsequent dehydration.

Funke (1983) suggested that mould is the most troublesome form of microbial invasion when artificially rearing insects. Microbial invasion usually causes spoilage (Ludemann *et al.* 1979) or alters the biological performance of the insect (Singh & House 1970). The most common microbial invaders of artificial diets are *Aspergillus* yeasts, *Rhizopus* bacteria and *Penicillium* moulds (Funke 1983; Singh 1984). Antimicrobial chemicals have been reviewed by Singh & House (1970), Ludemann *et al.* (1979), Funke (1983) and others.

Although mould invasion was not always fatal, it might be a major problem for future attempts to mass rear *A. ptyoptera*. The most likely source of infection in the diet is the larvae. If a diet suitable for *A. ptyoptera* is developed, this source of infection may be avoided by sterilizing eggs (by washing in detergent and sterilizing solutions (Singh 1984)) and grafting the neonate larvae to the diet.

Despite the high mortality rate in the artificial diet culture, and other problems, the results are promising. Just over a third of the specimens, including a few from relatively small larvae, successfully completed development and were fertile. These results suggest: i) *A. ptyoptera* is can be successfully reared on artificial diet, ii) although some properties of GPD may not be appropriate, it is nutritionally adequate; and iii) with greater expertise, superior equipment and perhaps a more complete understanding of the environmental needs and tolerances of *A. ptyoptera*, mass culturing of this agent is possible. If current host specificity trials (Hill *et al.* unpub.) indicate that the species merits further consideration, the development of an artificial rearing technique will be justified.

### 5.3.4 Sub-Section Summary

Almost all preliberation exercises in biocontrol are greatly facilitated if the agent can be artificially reared. However, the long development period and stem-mining habit of *A. ptyoptera* have hindered attempts to rear it.

The various methods used to obtain adults fall into two groups: i) methods that rely on field collected specimens; and ii) culturing larvae on artificial diet.

The most efficient of the field collection methods was to place whole branches in perspex incubators. However, field collection methods were laborious and unreliable. They are also not suited to rearing *A. ptyoptera* in quarantine or any subsequent mass rearing.

Rearing larvae on general purpose artificial diet (Singh 1983) gave moderately successful results. The major sources of mortality in the culture are believed to be the diet being initially unsuitable for establishment and the deterioration of the diet before development was complete.

However, the results are promising in that they indicate *A. ptyoptera* can be artificially reared. With a more complete understanding of the environmental requirements of *A. ptyoptera* and a more managed use of artificial diet, mass rearing is probably possible.

## 5.4 Host Specificity

### 5.4.1 Introduction

When undertaking classical weed biocontrol, before a natural enemy can be released it is usually necessary to demonstrate beyond reasonable doubt that desirable plants will not be attacked, i.e., is the agent safe? Traditionally, host specificity has been the pivotal point in gaining approval for the release of any weed biocontrol candidate. The ideal agent feeds only on the target weed, but a defined host range that includes more than one species is usually tolerated, so long as none are of value. When undertaking biocontrol programmes using new associations (see Section 5.1), this traditional approach to host specificity is likely to need some re-evaluation.

Host specificity is a term used to describe the breadth of diet of a consumer. The aim of host specificity screening is to quantify the host range of potential biocontrol agents. The diet breadth of herbivorous insects ranges from "restricted" monophages at one extreme to polyphages at the other. There are many interpretations of the terms monophagous and polyphagous (see May & Ahmad 1983; Strong *et al.* 1984). For this study, polyphagous insects are defined as those whose host range includes members of taxonomically distinct families. Oligophagous species feed on several members of one family, and monophages are those which feed on one species or species group. Restricted monophages are restricted to single species or biotype (Harris 1973).

As this study largely concerns the investigation of biological parameters considered before host specificity determination is begun, host specificity *per se* is not examined. However, certain areas of host specificity are considered. These are:
i) the plant species on which *A. ptyoptera* is known to feed on in New Zealand (i.e., the host range) and the phenomenon of host transference;
ii) an evaluation of possible techniques for determining host specificity of *A. ptyoptera*; and
iii) the risk of unexpected host shifts.

### 5.4.2 Materials and Methods

Of the three items given above, only i) and ii) involved experimentation and gathering otherwise unavailable information. Item iii) is a brief review of the literature concerning the risk of host transference in weed biocontrol insects, along with some personal observations.

The host range of *A. ptyoptera* was partially investigated through information from Mr J. S. Dugdale, DSIR Plant Protection, Auckland (the information source of Butler (1979)); Ms P. Syrett, DSIR Plant Protection, Lincoln; Mr Maurice O'Donnell, MAF Quality Management, Lincoln; Mr Brian Patrick, DOC, Dunedin; as well as the institutions listed in 4.2.2.

The other approach used in investigating the host range was to monitor the extensive planting of "New Zealand brooms" (the tribe Carmichaelieae) at DSIR Land Resources, and various other plants, for *A. ptyoptera* damage. The species present in the DSIR gardens and the other species examined are listed in Table 5.3. The DSIR garden was planted at various dates from 1978-1980. An *A. ptyoptera* population has been present since before March 1988 (pers. obs.). In November 1989, the entire New Zealand broom collection was inspected for *A. ptyoptera* damage. This natural experiment had further depth in having the legumes *Sophora microphylla, S. prostrata, S. tetraptera, S. tetraptera* var. *howinsular* and *Clianthus puniceus* growing adjacent to the *A. ptyoptera* infested broom plots. These species were also inspected for *A. ptyoptera* damage or signs, i.e., die-back and/or frass. Extraction to confirm the identity of larvae from these plants was not possible, because to remove stem-borers is necessarily destructive.

For the various plant species considered in the host range, the following system of classification was used.
"Confirmed" = plant species from which *A. ptyoptera* was extracted.
"Strongly suspected" = species on which signs of damage and evidence of stem-mining that resembled that of *A. ptyoptera* were found, but the presence of *A. ptyoptera* was not confirmed.
"Suspected" = plant species which other researchers have found or suspected to be hosts, but for which confirmation is lacking.
"Possible" = plant species that are considered possible hosts but were not examined.
"Apparently not" = species that were examined and no evidence of *A. ptyoptera* was found.

It was envisaged that the appropriate method of testing the host specificity of *A. ptyoptera* would be a triple tiered system comprising: i) oviposition preference testing in small arenas; ii) oviposition testing in large field cages; and iii) larval starvation tests.

To allow speedy execution of the host specificity screening that is proposed to follow this study, various techniques for use in the first and third tiers were developed and assessed. In addition, a provisional list of test plant species for exposure to *A. ptyoptera* was compiled.

The technique adopted for the small arena oviposition testing was a modification of a technique first developed by Frick (1970) and used by Hill & O'Donnell (in prep.) for testing *Agonopterix ulicetella,* another gorse control candidate. This test is effectively three tests: a pair (= a gravid female) was first exposed to the host and test species simultaneously (i.e., a "choice" test). After a specified period (using data from the fecundity trials (see Section 4.5) seven days was deemed appropriate for *A. ptyoptera*), the number of eggs laid on each species and on the cage was recorded. Then the female was given "no choice", i.e., exposed to the test species only, for the same period of time. As a control for the "no choice" test, the choice test was then repeated.

*Genista lydia* and *Lupinus arboreus* (both Faboideae) were selected as the test plants in the development of host specificity trials. Both species are, like gorse, in the tribe Genisteae. Within the Genisteae, *Genista* is the closest relative of the *Ulex* genus and *Lupinus* is the most distant (Bisby 1981). Thus these two species

were chosen to give both a vigorous test of the specificity of *A. ptyoptera* and perhaps an indication of the breadth of host discrimination *A. ptyoptera* can express.

Two methods of small arena oviposition test were assessed: i) 500 x 500 mm nylon gauze cages containing whole potted plants. Cotton wool dental rolls soaked in a honey-water solution were placed in the cages and the plants watered every three days. ii) 190 tall x 200 mm diameter cylindrical ventilated plastic "biscuit barrels". In these biscuit barrels, the plants were presented as 100 - 150 mm cut shoots standing in 40 x 20 mm vials of water. The shoots were inserted through a closed cell foam bung that was inserted in the top of the vials. The vials were stabilised by standing them in holes cut in a 30 x 200 mm strip of closed cell foam and placed in the bottom of the barrel. The honey water was again made available to the moths.

For the larval starvation assessment, neonate larvae were introduced to plants using the method described in Section 4.3. Eggs were carefully removed from the surface of plants used in the oviposition trials. Between 5-30 eggs were placed in open gelatine capsules that were then tied to the stems of the test plants or the gorse controls, allowing the neonate larvae to disperse naturally. The above test was repeated five times for each test plant species, and each replicate had a gorse control using eggs from the same batch.

### 5.4.3 Results and Discussion

#### 5.4.3.1 Host Range

An insect's host range may be defined as those plants on which it completes normal development in nature (Hanson 1983). The host range of *A. ptyoptera* is shown in Table 5.3, along with suspected and possible hosts and other members of the Faboideae that were examined. The only species from which I was able to isolate *A. ptyoptera* larvae were gorse and *Carmichaelia robusta*; therefore these are taken as the only confirmed hosts. However, some other members of the Carmichaelia genus are almost certainly also hosts.

*Carmichaelia* is a genus of 39 species indigenous to New Zealand with the exception of *C. excelsa* (endemic to Lord Howe Island) (Allan 1982). Members of the genus occupy an extraordinarily wide range of habits. Mature *Carmichaelia* show degrees of leaflessness, and the flattened branchlets perform transpiration and photosynthesis (Slade 1952). Due to a high level of intraspecific variation and indistinct species boundaries, the taxonomy of *Carmichaelia* is complex and confused. The occurrence of distinct geographical (P. Heenan pers. comm.) and chemotaxonomic types (Purdie 1984) indicate a need for the revision of the genus. Using the current taxonomic system, *C. robusta* is the most common *Carmichaelia* species in Canterbury.

**TABLE 5.3: Host range of *A. ptyoptera*, including suspected and possible hosts. KEY: "Confirmed" = confirmed record; "Strongly Suspected" = evidence found but not confirmed; "Suspected" = observation of another researcher but observation not confirmed; "Possible" = never examined or recorded but considered possible host; "Apparently not" = species examined and no evidence found, considered unlikely to be host.**

| | |
|---|---|
| **FAMILY: Fabaceae** | |
| **SUB FAMILY: Faboideae** | |
| **TRIBE: Sophoreae;** | |
| *Sophora tetraptera* | **Remotely possible?/ Apparently Not** |
| *Sophora microphylla* | **Apparently Not** |
| *Sophora prostrata* | **Apparently Not** |
| **TRIBE: Galegeae;** | |
| *Clianthus puniceus* | **Suspected** |
| **TRIBE: Carmichaelleae;** | |
| SUB GENUS: Carmichaelia; | |
| *Carmichaelia aligera* | **Possible?** |
| *C. appressa* | **Strongly Suspected** |
| *C. arborea* | **Strongly Suspected** |
| *C. cunninghamii* | **Apparently Not** |
| *C. egmontiana* | **Apparently Not** |
| *C. flagelliformis* | **Apparently Not** |
| *C. hookeri* | **Apparently Not** |
| *C. ovata* | **Strongly Suspected** |
| *C. robusta* | **Confirmed** |
| *C. ramosa* | **Strongly Suspected** |
| *C. solandri* | **Apparently Not** |
| SUB GENUS: Enysiella | |
| *C. orbiculata* | **Possible** |
| SUB GENUS: Huttonella | |
| *C. compacta* | **Strongly Suspected** |
| SUB GENUS: Kirkiella | |
| *C. kirkii* | **Strongly Suspected** |
| SUB GENUS: Petriea | |
| *C. petriei* | **Strongly Suspected** |
| *C. virgata* | **Strongly Suspected** |
| SUB GENUS: Thompsoniella | |
| *C. odorata* | **Possible/ Apparently Not? (1 Rep.)** |
| *Chordospartium muritai* | **Apparently Not** |
| *Chordospartium stevensonii* | **Apparently Not** |
| *Corallospartium crassicaule* | **Suspected/ Apparently Not? (1 Rep.)** |
| *Notospartium glabrescens* | **Apparently Not** |
| *Notospartium carmichaeliae* | **Apparently Not** |
| *Notospartium torulosum* | **Apparently Not** |
| **TRIBE: Genisteae;** | |
| *Lupinus arboreus* | **Apparently Not** |
| *Cytisus scoparius* | **Suspected** |
| *Genista lydia* | **Apparently Not** |
| *Ulex europaeus* | **Confirmed** |

The plants thought to be hosts are listed in Table 5.3 as "strongly suspected". They are all within the genus *Carmichaelia*, but do not include all members of that genus. Notably the *Carmichaelia* species that are "apparently not hosts" (i.e., *C. cunninghamii, C. egmontiana, C. flagelliformis, C. hookeri, C. solandri*) are all North Island species (Purdie 1984) within the sub-genus *Carmichaelia*. *C. aligera* is the only North Island member of the sub-genus *Carmichaelia* that is considered a possible host because one *C. aligera* of the Lincoln specimens (out of approximately 40) had damage resembling *A. ptyoptera* feeding. In contrast, all the South Island *Carmichaelia* (including those in the other sub-genera) are "strongly suspected" hosts. (It should be noted that the biochemical differences between some of the sub-genera may actually be slight or non-existent (Purdie 1984)).

Although no records have been found of *C. orbiculata* as a host, it is a "possible" host because an *A. ptyoptera* specimen has been reared (thus confirming the identity of the moth) from '*Carmichaelia* sp.' on the Desert Road, Tongariro (M. Nuttal, FRI, Rotorua, pers. comm.), and *C.orbiculata* is one of only three *Carmichaelia* in that region (Allan 1982; Purdie 1984). The other New Zealand brooms from the Desert road/Tongariro Plateau region are *C. odorata* and *C. flagelliformis*. Although the one specimen of *C. odorata* I examined had no *A. ptyoptera* damage, it is considered a possible host for the reason given above. No damage was found on the 21 *C. flagelliformis* plants examined, so it was classified as apparently not a host.

The *Chordospartium, Corallospartium* and *Notospartium* specimens at Lincoln were not attacked. However, *A. ptyoptera* larvae have reportedly been extracted from *Corallospartium*, so it is a suspected host (see discussion below). Notwithstanding this possibility, *A. ptyoptera* has at least a moderate degree of specialisation within the tribe Carmichaelieae.

Species from which other people have reportedly found *A. ptyoptera* are the following: i) "Boring in *Clianthus puniceus*" - Collector unknown; Palmerston, DN; determined by J.S. Dugdale; collection record from MAF Quality Management, Lincoln, correspondence file; specimen not seen); ii) "*Corallospartium* sp." - J.S.Dugdale personal observation; 'near Porters Pass' MC; specimens not seen); and iii) *Cytisus scoparius* - P. Syrett personal observation; Canterbury; single damaged specimen tentatively identified by W. Thomas but longer exists (i.e., not seen).

None of these records have been confirmed. Although *A. ptyoptera* has been able to transfer from Carmichaelieae to gorse (within the Genisteae), *Clianthus puniceus*, within the Galegeae, would presumably be a difficult chemotaxonomic step (Polhill & Raven 1981) to make for an insect that expresses a moderately narrow range within its original tribe (although Galegeae and Carmichaelieae do have several features in common (Polhill & Raven 1981)). Further, *C. puniceus* is an ornamental widely grown in New Zealand and *A. ptyoptera* has been reported on it only once. This tends to support the possibility that the larva was misidentified.

The *Corallospartium crassicaule* record is more reliable, given that this species is within the tribe Carmichaelieae and that Slade (1953) suggested *Corallospartium* could be reduced to a sub-genera of *Carmichaelia* (i.e., they are close). However, the plant may have been misidentified by the collector: the growth forms of *C. crassicaule* and some *Carmichaelia* are not dissimilar, and confusion between the two is possible.

The record of *A. ptyoptera* on *Cytisus scoparius* is perhaps the least reliable of the three "suspected" hosts. The one larva found was damaged on extraction, making the identification more difficult than it would have already been (see Section 3.1). Further, the fact that there is only one tentative *A. ptyoptera* recovery from the hundreds of hours spent examining *C. scoparius* by Syrett and other DSIR Plant Protection members argues against *C. scoparius* being a host. In addition, the suitability of *C. scoparius* as a host is doubted because of the defensive chemicals it contains (Smith 1966; Wink *et al.* 1982).

A further complexity encountered when examining the host range of *A. ptyoptera* was the remote possibility of *Sophora tetraptera* being a host. Given the economic and cultural importance of *Sophora chrysophylla* in Hawaii (Po-Yung Lai pers. comm.), this possibility is of critical importance with regard to the use of *A. ptyoptera* as a biocontrol agent there. *S. tetraptera* has arisen as a "remotely possible" host because of the recovery of two *A. ptyoptera* specimens (C. Muir; Riccarton Bush, Christchurch MC) which differ from other specimens in that the valva has a "apical thorn only, not a.t. and stiff bristles" (J. Dugdale pers. comm.). Dugdale suggested they might be from a '*Sophora* feeding population'. However, despite intensive searching of the *Sophora* trees at Riccarton Bush, as well as *S. tetraptera* and *S. microphylla* plants growing amongst *A. ptyoptera* populations in three Canterbury locations, no sign of *A. ptyoptera* damage or feeding was been found. I doubt *Sophora* is a host.

Given the morphological differences of the Riccarton Bush specimens, they may belong to a "sibling species" and not *A. ptyoptera* as we know it. The taxonomic position of these specimens is currently undecided (Dugdale pers. comm.).

**Host Transference**

As shown in Table 5.3, the confirmed hosts of *A. ptyoptera* occur within two distinct tribes. As noted in Section 5.1, *A. ptyoptera* attacking gorse constitutes a "new association". A notable aspect of this new association is the chemotaxonomic distance between the the original and novel hosts.

As one might expect with the diversity, abundance, academic and economic importance of insect plant associations, the body of literature concerning host shifting is large. However, our poor understanding of host plant location and selection along with other aspects of insect-plant relationships has allowed only a few satisfactory hypotheses and generalisations to be made.

Strong *et al.* (1984) reviewed some of the current explanations for host shifts. They suggested that host shifts appear to occur *via* two paths: i) although most host shifts involve polyphages (Strong *et al.* 1984), occasionally apparently mono and oligophagous insects may unpredictably include a taxonomically distant, or even unrelated, host into their diets because of the two plant species may have a common occurrence of various chemicals unrelated to their taxonomic affinity; alternatively ii) many novel hosts have no obvious structural or biochemical affinities and the new associations appear to have arisen because of the close physical proximity of the normal host and the new host species, i.e., ecological opportunity.

The host shift of *A. ptyoptera* onto gorse can be assigned to either or both of the above routes. The Canterbury plains were colonised by Europeans and converted to agricultural use in the 1850s (Hilgendorf 1927). Gorse was and is extensively used for fencing (Hill pers. comm.). As agriculture (including gorse) replaced the natural vegetation and gorse became a widespread weed, presumably contact between gorse and *A. ptyoptera* would have been regular. Indeed gorse is now far more abundant in mid-Canterbury than *Carmichaelia*, and gorse was and is probably the most frequently encountered woody legume.

In addition to the ecological opportunity presented by the apparency (*sensu* Feeney 1976) of gorse, this host shift may have been facilitated through gorse being both biochemically and structurally acceptable, possibly due to its relatively close taxonomic position. As noted in Section 4.3, at most times of the year gorse has only a relatively low amount of defensive chemicals (Hill 1982), and it probably did not present a major detoxification hurdle. However, overcoming the low N levels of gorse may have been more problematic. Although the tissues of gorse appear to be nutritionally and structurally adequate for *A. ptyoptera* development, to successfully exploit gorse it may have been necessary to develop the specialised feeding strategy of feeding in N rich parts of the plant. Alternatively, such a strategy may have already been present, and the shift was relatively straightforward.

In addition to these two possible causes, another which may have contributed to this host shift is a possible reduction in various mortality factors associated with the traditional host (Thomas pers. comm.). For example, the initial shift may have given better survival to the variant population because it temporarily escaped its presumably habitat specific parasitoids (see Section 4.4).

At the level of the individual, possible mechanisms for the initial step in multiple host use include: i) a few females of some mono - oligophagous species behave as generalists when ovipositing, and show very little discrimination between the true host and other species (Singer 1982; Crawley 1983); and ii) if the true host is sufficiently rare and localised, many searching insects will not encounter it. Eventually less preferred hosts will become acceptable (Singer 1983). Given: i) the scarcity of *Carmichaelia* (in Canterbury at least) in relation to the abundance of gorse; and ii) the apparent ability of *A. ptyoptera* to oviposit on non-hosts (see Section 5.4.3.2), either of the above mechanisms may have contributed to this host shift.

Whichever the mechanism, or combination of mechanisms, from which this host shift evolved, for the "shifted population" to be maintained, it is thought the shift would have needed to have given higher

fitness. Because of the sympatric distribution of gorse and *Carmichaelia*, the variants must presumably have achieved greater survival, or this behaviour would have been eliminated through gene flow (Rausher 1984). Alternatively, the gorse feeding variants may have been initially isolated from the "normal" population, perhaps by rigid host-plant selection (i.e., allopatric differentiation) and so long as population growth was positive, the variant population may have accumulated adaptations until it eventually adapted sufficiently for the population to flourish.

The above possibilities imply that the host switch has been the result of gorse occurring within the dietary range of *A. ptyoptera*, and the switch would have involved minor behavioural modifications. An alternative is that the shift in host plants involved an evolutionary component, i.e., *via* genetic mutation or variation. If this is the cause of the new association, one might expect more genetic variation in the variant population and hence the ability for further host shifts may be maintained. This is probably the most perplexing yet important issue facing those advocating "new associations" in biocontrol. Although well designed host specificity experiments can demonstrate the current diet breadth of an insect (see Section 5.4.3.2), the risk of unexpected host shifts is more difficult to quantify (see Section 5.4.3.3).

One aspect that suggests a genetic component may have been involved in the host shift of *A. ptyoptera* is that although the species occurs throughout most of New Zealand, the new association has only been found in Canterbury and Otago (see Section 5.5). However, it is unknown if local differences in host specificity (Fox & Morrow 1981) arise from variation in traits of insects or of plants (Thomas *et al.* 1987). Therefore, an equally likely explanation is that local differences in the plants and/or environmental parameters have driven this host shift, without a change in the genetic make-up of *A. ptyoptera*. The possible explanations for this divergence in behaviour within the sub-divided *A. ptyoptera* population are discussed in Section 5.5.

### 5.4.3.2. Host specificity testing

Another objective of this study was to develop a technique for assessing the host specificity of *A. ptyoptera*, or at least to eliminate some methods as unsuitable. Specificity is not only related to adult feeding, it also encompasses the ability to develop eggs and the capacity of larvae (first instar and later stages) to establish and develop on various plants. Important determinants of specificity in phytophagous insects include behavioural (e.g., feeding habit) and physiological (e.g., the ability to detoxify the defensive chemicals of one's host as well as utilise its nutritional peculiarities) adaptations, as well as phenological sychronisation of life histories. Other factors believed to influence the host range of an insect are processes involved in host plant finding, recognition and acceptance of the plant for feeding or oviposition (e.g., Dethier *et al.* 1960; Dethier 1982; Miller & Strickler 1983).

A herbivorous insect-plant associations is demonstrated by the insect feeding and/or ovipositing on the host plant. Using this association, early researchers developed the starvation and negative oviposition tests. In a starvation test an insect is given the choice of starving to death or feeding on selected non-host test plants.

Similarly, oviposition tests examine the ability of gravid females to oviposit on a series of test plants when confined to them.

Because starvation and negative oviposition tests confine the insect to artificial environments, their complete array of host locating and discriminating behaviours are unable to be used. Increasing the size of the cage may produce valid results for some species (Harley 1968), but for many insects, contact with any barrier disrupts behaviour (Cullen in press). Dunn (1978) suggested the "partial cage" as a compromise. However, this method is limited by valuable insects escaping and by quarantine considerations. So, because we are stuck with the cage, it is important to ensure that the other components of the cage environment are as natural as possible. Attention needs to be paid to the size and shape of the cage (maximum size and least obstructive structure possible), light (quality and photoperiod), temperature and humidity. For development of larvae and oviposition, size and quality of the plant (it should be hardened off outside) is also important.

Another aspect of the insect's natural environment not available in laboratory starvation tests is choice. As a result, non-hosts are often selected as oviposition or feeding sites. Hence starvation tests have been criticised as indicating a wider host range than occurs in the field (e.g., Frick & Andres 1967) and/or giving information of little biological meaning (Dunn 1978; Martinat & Barbosa 1987).

Nevertheless, as pointed out by Cullen (in press), starvation tests do indicate a physiologically possible host range, and can be carried out in quarantine. Indeed, these tests continue to form the basis of most host specificity screening.

As outlined in section 2.4.4.2, more meaningful results can be derived from choice tests. Although, choice tests also have the disadvantage of confining the insect, as well as other complications (see Section 2.4.4.2; Cullen in press).

The technique used in examining the oviposition preference of *A. ptyoptera* consisted of both choice and no-choice, i.e.,

| | | | |
|---|---|---|---|
| Choice: | Ulex | Test plant | 7 days |
| No-Choice: | - | Test plant | 7 days |
| Choice: | Ulex | Test plant | 7 days |

The results from these tests using the two different small arenas - nylon gauze cages and plastic "biscuit barrels" - are shown in Table 5.4.

The nylon cages are an inappropriate method because of the large number of replicates in which no eggs were laid. Further, although these cages were relatively spacious and whole plants could be enclosed (albeit small ones), the amount of time need to examine the plants in each replicate and the cage (up to 4 hours) is impractical.

**TABLE 5.4: Results from small arena oviposition tests using two types of cages: oviposition by paired *A. ptyoptera* females when presented with i) gorse and one of two test plant species; and ii) the test species only. * = no-choice does not have control (i.e., no eggs laid in period three).**

| Nylon cages | Test | Eggs laid on gorse | Eggs laid on test plant | Eggs laid on container |
|---|---|---|---|---|
| **Gorse present - choice test (period one)** | | | | |
| *Genista lydia* | 1 | | No eggs laid. This replicate discontinued | |
| | 2 | 14 | 0 | 0 |
| | 3 | 21 | 4 | 0 |
| | 5 | 13 | 9 | 0 |
| | 7 | | No eggs laid. This replicate discontinued | |
| | 8 | | No eggs laid. This replicate discontinued | |
| *Lupinus arboreus* | 4 | | No eggs laid. This repicate discontinued | |
| | 4a | | No eggs laid. This replicate discontinued | |
| | 6 | | No eggs laid. This replicate discontinued | |
| | 9 | | No eggs laid. This replicate discontinued | |
| | 10 | 9 | 7 | 0 |
| **Gorse absent - no choice test (period two)** | | | | |
| *Genista lydia* | 3 | - | 5 | 0 |
| | 5 | | Female died before period two completed. | |
| *Lupinus arboreus* | 10 | | Female died before period two completed. | |
| **Gorse present - choice test (period three)** | | | | |
| *Genista lydia* | 3 | 19 | 0 | 0 |
| *Lupinus arboreus* | | | | |

| "Biscuit barrels" | Test | Eggs laid on gorse | Eggs laid on test plant | Eggs laid on container |
|---|---|---|---|---|
| **Gorse present - choice test (period one)** | | | | |
| *Genista lydia* | 11 | | No eggs laid. This replicate discontinued | |
| | 12 | 30 | 0 | 32 |
| | 14 | | No eggs laid. This replicate discontinued | |
| | 16 | 57 | 0 | 0 |
| | 18 | 3 | 0 | 0 |
| | 19 | | No eggs laid. This replicate discontinued | |
| | 22 | 25 | 4 | 0 |
| | 24 | 44 | 0 | 0 |
| *Lupinus arboreus* | 13 | 39 | 18 | 0 |
| | 15 | 15 | 0 | 4 |
| | 17 | 30 | 13 | 0 |
| | 20 | | No eggs laid. This replicate discontinued | |
| | 21 | 32 | 6 | 0 |
| | 23 | 23 | 0 | 0 |
| | 25 | 48 | 0 | 0 |
| **Gorse absent - no choice test (period two)** | | | | |
| *Genista lydia* | 12* | - | 5 | 0 |
| | 16 | - | 7 | 0 |
| | 18 | | Female died before period two completed. | |
| | 22* | - | 7 | 0 |
| | 24 | - | 4 | 0 |
| *Lupinus arboreus* | 13 | - | 107 | 1 |
| | 15 | | Female died before period two completed. | |
| | 17 | - | 17 | 0 |
| | 21 | - | 5 | 0 |
| | 23* | - | 0 | 0 |
| | 25 | - | 14 | 0 |
| **Gorse present - choice test (period three)** | | | | |
| *Genista lydia* | 12 | 0 | 0 | 0 |
| | 16 | 18 | 0 | 0 |
| | 22 | 0 | 0 | 0 |
| | 24 | 19 | 0 | 0 |
| *Lupinus arboreus* | 13 | 38 | 5 | 0 |
| | 17 | 19 | 0 | 0 |
| | 23 | 0 | 0 | 0 |
| | 25 | 4 | 0 | 0 |

The reason for the poor performance of *A. ptyoptera* in the nylon cages is unknown. However, given the relatively abundant oviposition in the fecundity trial containers (see Section 4.5), it is suspected that the cages were unable to maintain sufficient humidity. The quality of light may have also been sub-optimal in these cages, for inside these cages the far-red is doubled (Gassen pers. comm.). As well as altered spectral quality, increase in far-reds increases temperature and decreases humidity.

In contrast to the nylon cages, at least some oviposition occurred in most of the biscuit barrels. However, the 21 day sequence of tests proposed was completed in only a third of the replicates. A problem encountered in both arenas was the low longevity of the adults. This factor is partially responsible for many of the no-choice tests being invalid because no oviposition occurred in "period three", i.e., the no-choices are without controls.

As the proposed choice/no-choice sequence appears to be hard to achieve, an alternative is to conduct oviposition tests consisting of only the initial choice period. However, given the doubts raised by this being a new association, it is suggested the more thorough test is appropriate. Yet because the above test is expensive in the number of adults needed and time consuming (16-20 days over eight weeks), screening all test species within one or two seasons is unlikely unless artificial rearing is achieved (see Section 5.3).

The test species used are close relatives of gorse, and therefore provide a very vigorous test of the discriminatory abilities of the moth (Hill pers. comm). Nevertheless, the biscuit barrel results indicate that *A. ptyoptera* can discriminate in these small arenas. In the choice tests, 40 times as many eggs were laid on gorse as on *G. lydia* and five times as many eggs were laid on gorse as on *L. arboreus*.

**TABLE 5.5: *A. ptyoptera* neonate larval establishment results from some starvation tests.**

| | Test plant | | | Gorse control | | |
|---|---|---|---|---|---|---|
| Test species | Eggs per bush | Number of larvae estb. | Most advanced life stage | Eggs per bush | Number of larvae estb. | Most advanced life stage |
| *G. lydia* | 5 | 0 | Nil | 6 | Plant died | |
| *G. lydia* | 7 | 0 | Nil | 7 | 6 | Instar V? |
| *G. lydia* | 15 | 1 possible | L1 - very small gallery and no larva found | 15 | 7 | Plant died |
| *G. lydia* | 15 | 0 | Nil | " | " | " |
| *G. lydia* | 20 | 0 | Nil | 10 | 7 | Instar III? |
| *L. arboreus* | 10 | 0 | Nil | 10 | 7 | Plant died |
| *L. arboreus* | 18 | 0 | Nil | 15 | 6 | Adult |
| *L. arboreus* | 20 | 0 | Nil | " | " | " |
| *L. arboreus* | 30 | 0 | Nil | 30 | Plant died | |
| *L. arboreus* | 30 | 0 | Nil | 30 | 5 | Adult |

The results from the starvation tests are shown in Table 5.5. The high rate of establishment on the gorse controls confirm that this method is suitable in the starvation screening of *A. ptyoptera*. However, this method is not suited to testing herbaceous species that might need to be tested - although the "woody-stem boring" habit of *A. ptyoptera* may make these test species irrelevant. The number of larvae that established and survived indicate that 10 eggs is a good number to successfully inoculate the plants.

The lack of establishment (none confirmed) on the test species indicate that *A. ptyoptera* neonate larvae do not perform well on the other members of the Genisteae. This suggests that within this tribe, *A. ptyoptera* may be physiologically restricted to gorse, although several more species remain to be tested.

**Test Plants**

The current method of host specificity screening is to determine which plants the candidate *can* and *does* attack and/or complete development on (cf. the negative "crop testing" method) and if possible, to isolate the reasons for host restriction (Harris 1963; Wapshere 1974a, b). This approach relies on both experimental interpretation and empirical evidence from the literature (Harris and Zwolfer 1968). In this project, like other contemporary weed biocontrol projects, the method used to select test plants is the "centrifugal phylogenetic" method and its associated "safety net", as described in Section 2.4.4.2.

**TABLE 5.6: Suggested test plants for host specificity screening.**

| Species | Family/ Tribe |
|---|---|
| *Genista* sp. | Fabaceae (Faboideae)/ Genisteae |
| *Teline monspessulanus* | |
| *Spartium junceum* | |
| *Calicotome spinosa* | |
| *Chamaecytisus palmensis* | |
| *Cytisus scoparius* | |
| *Cytisus multiflorus* | |
| *Lupinus arboreus* | |
| *Crotalaria* sp. | Crotalarieae |
| *Erythrina* sp. | Phaseoleae |
| *Carmichaelia* spp. | Carmichaelieae |
| *Corallospartium crassicaule* | |
| *Robinia* sp. | Robinieae |
| *Sutherlandia* sp. | Galegeae |
| *Colutea* sp. | |
| *Clianthus puniceus* | |
| *Sophora* spp. | Sophoreae |
| *Hoheria* spp. | Malvaceae |
| *Plagianthus* spp. | |
| *Hibiscus* spp. | |

Plants suggested for inclusion in the host specificity screening of *A. ptyoptera* are listed in Table 5.6. This list is arranged from the closest relative of gorse to progressively more distantly related species (according to Polhill & Raven (1981)).

Members of the Genisteae are included as the first sequence of the phylogenetic selection (see Wapshere 1975; CABI 1986). *Cytisus scoparius* is also included because it is a "suspected" host (see Section 5.4.3.1). *Crotalaria* and *Robinia* are included because they exist in Hawaii (St. John 1973) and are in tribes that are taxonomical neighbours of New Zealand hosts. *Sophora* is included because of the remote possibility that it may be a host, and because of the many endemic forms in Hawaii (St John 1973; Rock 1974). *Erythrina* is another Hawaiian endemic within the Faboideae (Rock 1974). *Sutherlandia* and *Colutea* are Hawaiian members of the Galegeae, which also contains the suspected host *Clianthus puniceus*. The only genera in the list outside the Faboideae are *Hoheria, Plagianthus,* and *Hibiscus*. These genera are included because they are the hosts of the other *Anisoplaca* species (Dugdale pers. comm.).

### 5.4.3.3 The Risk of Unexpected Host Shifts

The greatest risk posed when undertaking weed biocontrol is that the candidate agent might widen its host range to include new hosts in its diet. Lawton (1985) suggested there are at least two facets to this problem: i) what is the probability of an insect making an unexpected host shift? and ii) what is the correct evaluation of screening tests which reveal that the candidate has the ability to feed on other plants?

Several authors have discussed and discounted the risk of host shifts (Huffaker 1957, 1962; Harris & Zwolfer 1968; Zwolfer & Harris 1971; Dunn 1978; Batra 1981; Lawton 1985; CABI 1986). However, the probability of host shifts is not zero (Lawton 1985); insects do go onto novel hosts (Strong *et al.* 1984) and at least one situation exists where a biocontrol agent causes economic damage to a non-target host (Davies & Greathead 1967).

While minimising the risk of host shifts, weed biocontrol researchers have developed a relatively comprehensive ecological understanding of specificity. When searching for agents, workers must be aware that monophagy may be a local phenomenon (Fox & Morrow 1981). Attention must also be paid to variability of the agent population introduced. For these reasons, *A. ptyoptera* cultures for host specificity screening and export should all be sourced from the same locality (Hill *et al.* unpub.). Also, the specificity of the agent (as well as the efficiency of the program) rest on sound taxonomic skills (Debach 1964, 1974; Harris 1985) for both the identification of the target and selection of the agent, hence the detailed description of *A. ptyoptera* in Sections 2.2 and 3.1.

The issue of test plant acceptance in starvation tests also appears to have provided development of ecological theory (e.g. Dunn 1978; Andres 1981; Harris 1985; Cullen in press). Although test plant acceptance by agents from new associations (where the ability to shift hosts maybe maintained) does not appear to have been addressed.

Harris (1981b - cited in Harris 1985) proposed that the parameters that determine whether an insect species will damage a plant are: i) its ability; ii) the opportunity; and iii) the advantage of utilising it. The ability of an insect to exploit a plant does not mean it will attack that plant species in the field unless the other two

parameters are also positive. The opportunity of using the plant depends on the host finding and discriminating ability of the agent as well as its spatial and temporal coincidence with the plant (Harris 1985). The advantages of using a plant species are determined by the plant's abundance, its relative suitability as a food source, the insect's mortality on that plant (Thomas pers. comm.) as well as the intensity of interspecific competition from other phytophages (Holt 1977) or natural enemies (Lawton & Strong 1981; Strong *et al.* 1984).

In behavioural terms it appears that feeding on non-hosts in starvation trials arises from the plant being nutritionally adequate (or at least preferable to absolute starvation), and the hungry insect is responding to universally distributed substances such as sugar, water, nitrogen, etc., while, when faced with starvation, the advantages of overcoming the deterrents of a novel host are considerable, and therefore the attempt is likely to be made.

However, in the field, the threat to non-target plants is a function of the agent being able to locate and survive on the new host. The apparent inflexibility of insect behaviour has been relied on by many weed biocontrol workers when evaluating starvation trials. Thus belief has been reassured by work done by Futuyma *et al.* (1984) which suggested that divergence in host utilization occurs first *via* genetically determined changes in behaviour, rather than physiological adaptations to the novel host (see also Jermy 1984).

However, scepticism must still exist, for ovipositional mistakes do occur (Crawley 1983) and monophagous insects do adopt novel hosts (Strong *et al.* 1984). In the case of *A. ptyoptera*, because the candidate has made a multiple tribe host shift, we must proceed with considerable caution. Perhaps the most appropriate course will be to examine the performance of *A. ptyoptera* on a wide variety of critical plants, especially the "suspected" host species, followed by an especially stringent interpretation of the results.

### 5.4.4 Sub-Section Summary

Host specificity is the most severe constraint on the selection of weed biocontrol agents.

In this section various facets of the host specificity *A. ptyoptera* have been examined. *A. ptyoptera* is an oligophagous species. Although its host range is not clearly defined, it appears to include several *Carmichaelia* species within the tribe Carmichaelieae, as well as gorse, a member of the Genisteae, (also in the sub-family Faboideae) Some records suggest *A. ptyoptera* may occur on other species. These records may be spurious or incidental.

Of the two types of small arenas evaluated for oviposition testing, plastic biscuit barrels are considered the most appropriate. *Lupinus arboreus* and *Genista lydia* were used as test plants to evaluate a staggered test series consisting of: choice; no choice; choice, for use in small arena oviposition testing. These tests indicated that *A. ptyoptera* can discriminate in the small arenas. However, in many cases, the adults had

died before the test series was complete. Further, the limited availability of adults is likely to impede the execution of oviposition tests.

A starvation test method was developed in which neonate larvae were allowed to disperse naturally on whole test plants and controls. The results from these tests were very positive. This method is recommended as the most appropriate technique for the host specificity screening of woody plants.

The mechanism(s) by which the *A. ptyoptera*-gorse new association has arisen are not known. One of the many possibilities is that the host shift has arisen through genetic variation. If this is the case, the ability to shift hosts might be maintained. This possibility necessitates a cautious interpretation of any host specificity screening.

## 5.5 The Distribution of *A. ptyoptera*

### 5.5.1 Introduction

One thing common to most systems that have been proposed for assessing biocontrol candidates is an examination of the distribution of the candidate in its place of origin. As indicated in Section 2.4, the distribution of a candidate agent is taken as a measure of its ecological tolerance and adaptability.

The importance of the climate in both the native range and area of introduction has been widely discussed (e.g., DeBach & Bartlett 1964; Ehler & Andres 1983). Wapshere (1970, 1975, 1985) strongly advocated the importance of "eco-climatic matching" between the source of an agent and the area of introduction. However, the need for close climatic matching is not borne out by recent analysis of past weed biocontrol attempts (Hokkanen 1986; Crawley 1986, 1987). This is not to say biocontrol agents will tolerate extreme shifts in climates; it is almost certain they will not. This much is common sense, and hence most phytophagous biocontrol attempts have a reasonable to good climatic and photoperiodic match (Lawton in press). A detailed examination of a candidate's climatic distribution, as advocated by Wapshere (1985), may not be necessary: other aspects of a candidate's distribution are possibly equally important to its eventual performance.

Crawley (1986, 1987, 1989c) suggested that the extent of an agent's original range is positively related to the probability of it becoming established. However, exceptions exist and distribution appears to be linked to many aspects (see Gaston & Lawton 1988) which may also promote establishment. Nevertheless, wide geographic distribution probably indicates ecological tolerance and flexibility (Brown 1984). For this reason, the distribution of *A. ptyoptera* was examined.

*A. ptyoptera* is found only in New Zealand. Typical of most of our native moths, knowledge regarding the distribution of *A. ptyoptera* was limited.

### 5.5.2 Materials and Methods

Information on the distribution of *A. ptyoptera* in New Zealand was gathered in two ways. The first was the compilation of collection records from insect collections throughout the country. These sources were given in Section 4.2.2. Most of these records were of adults, and so the host plant concerned is unknown.

The second approach was to examine gorse bushes in parts of Northland-North Auckland, the environs of Wellington, the West Coast, Otago, Nelson and Marlborough and most of Canterbury. The following sampling method was used to determine the presence of *A. ptyoptera* in the gorse examined. *A. ptyoptera* damage is easily noticed and the initial part of each search consisted of 15 minutes looking for damage. If damage was encountered, the affected branch was dissected and cause of the damage ascertained, and specimens were recovered where they existed. If damage was not encountered, several branches were

chosen at random and roughly dissected to ensure the presence of any stem inhabiting insects had not been overlooked.

Information concerning the distribution of *A. ptyoptera* is given in Appendix Table IV.1 and summarized in Fig. 5.8. Geographical areas and abbreviations mentioned in the following discussion follow Crosby *et al.* (1976).

### 5.5.3 Results and Discussion

Examination of the distribution of *A. ptyoptera* has revealed a very interesting pattern. Although *A. ptyoptera* has been collected from throughout much of New Zealand (from latitude $37^0$S to $46^0$S), the *A. ptyoptera*-gorse association is restricted to Canterbury, Central Otago and part of the Dunedin region (see Fig. 5.8). The north and north-west boundaries of this pattern are distinct. The southern edge is close to the boundaries of CO-DN and SL and is less distinct, perhaps reflecting the lower concentration of gorse encountered in that area. The western edge of the "gorse area", believed to be in MK and OL, was not examined.

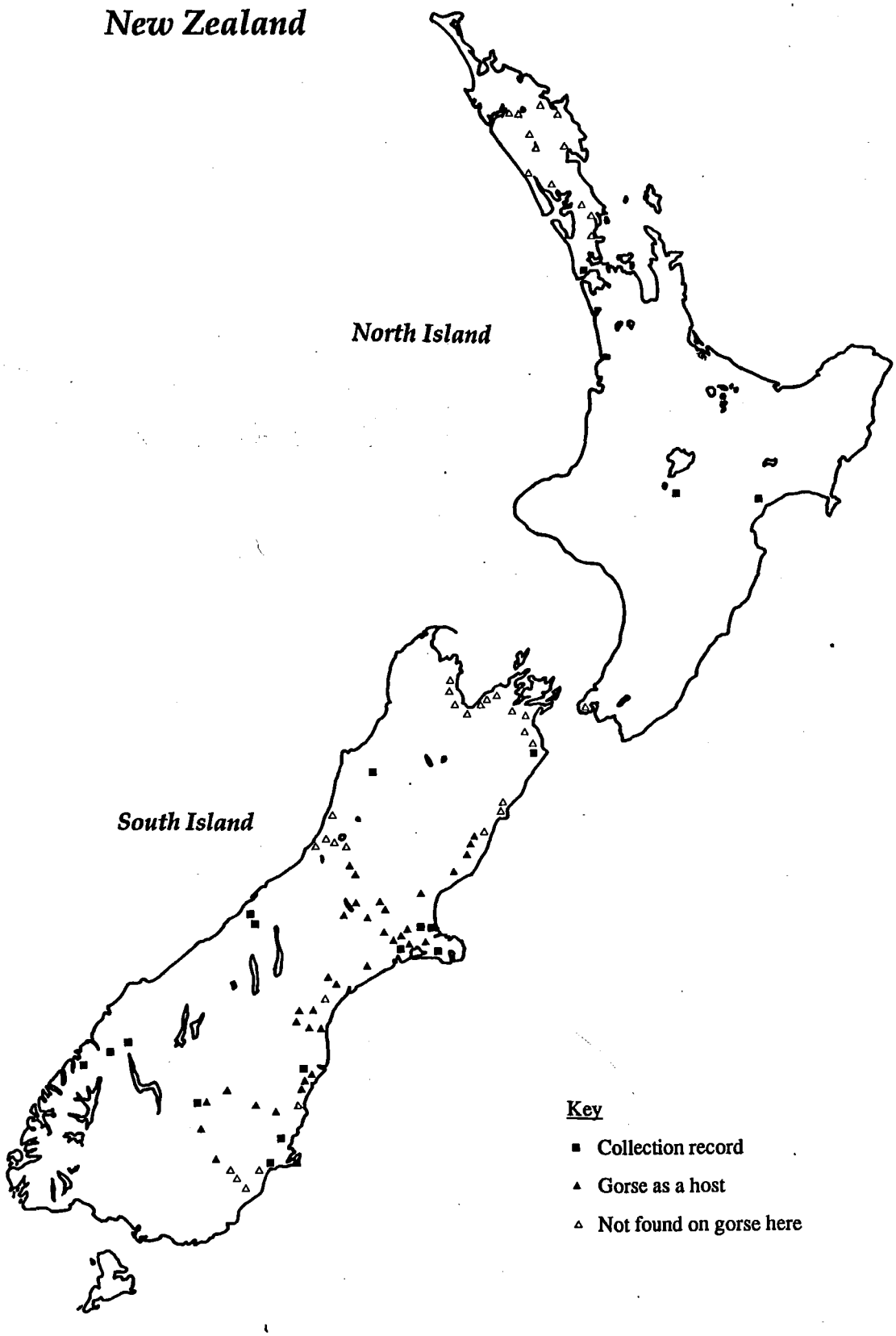
The region that was most extensively searched was mid-Canterbury. Within this region *A. ptyoptera* was found in all localities examined. The altitudinal range of *A. ptyoptera* (on gorse) within MC extends from below 50 m to over 700 m. Its range is largely in low rainfall areas, although the sites of some of the most eastern recoveries have moderate rainfall. It is unknown if a continuous distribution occurs in the other parts of the "gorse area". Although, the lack of "negative gorse recoveries" in these areas tend to suggest that its distribution might be fairly regular there also.

*A. ptyoptera* was not found on gorse in WD, SL, KA, NN, MB, nor, perhaps most importantly, in AK and ND, which are climatically similar to Hawaii. Given the likelihood that *A. ptyoptera* damage on gorse in other regions would have been reported, the extent of *A. ptyoptera*-gorse association shown in Fig. 5.8 is thought to be reliable. However, the distribution indicated may be biased by the uneven search pattern.

Possible explanations for this geographic divergence in behaviour within the *A. ptyoptera* population include: i) there may be a difference in host selection behaviour (possibly genetically determined) between Canterbury-Otago and other regions (cf. Rausher 1984, 1985; Thomas *et al.* 1987); or, ii) the moth populations in different regions are essentially the same and the different behaviours have arisen because of the environmental differences between the various regions; or iii) the gorse plants are sufficiently different between Canterbury-Otago and elsewhere, to allow colonisation by *A. ptyoptera* in the former areas only (cf. references in Thomas *et al.* 1987).

Investigating the above explanations was beyond the means of this study. However, some observations enable limited speculation. In Section 5.4 it was suggested a genetic difference might have been the mechanism by which the host shift arose. This hypothesis is supported by the finding that the use of gorse

**FIG. 5.8: The distribution of *A. ptyoptera* in New Zealand; including positive and negative recoveries from gorse**




P.W.H. 1990.

as a host is restricted to an area that probably has little gene-flow with other regions. To the west is the physical barrier of the Southern Alps. The northern boundary is around the Conway River - this area is also a transition zone for other insect species (e.g., the common grass cicada) (Dugdale pers. comm.), possibly due to the influence of the Seaward Kaikoura range. It is unknown if any barrier at the south end of the "gorse zone" exists. It is possible that SL is currently being invaded by the gorse feeding phenotype. This possibility is an alternative explanation for the discontinuous occurrence of *A. ptyoptera* on gorse found in that region.

Given the diversity of environments a species can inhabit, it is not surprising that wild populations consist of 'a wide variety of genotypes' (Hubby & Lewontin 1966). Indeed, I would expect the genetic makeup in Canterbury and Otago to be different from that of other regions. However, as other hypotheses can also explain the distribution pattern of gorse utilisation found, no conclusion can be drawn regarding the genetic maintenance of the ability to shift hosts and its associated dangers (see Section 5.4.3.3).

An alternative hypothesis is that the host shift is a function of the environment in Canterbury and Otago. The climates of these two regions are similar (hot, dry summers and cool winters). It may be argued that this weather pattern does not occur in other parts of New Zealand, or at least not to the same extent, and if the gorse feeding habit is due to environmental characteristics, one would expect it to be restricted to these areas. This possibility reflects poorly on the potential of *A. ptyoptera* as a biocontrol agent. The need for such an extreme climate would both limit its ability to establish and restrict the areas where it might be an effective control agent. However, the occurrence of the *A. ptyoptera*-gorse association in moderate rainfall areas like Lake Coleridge and Glenroy (MC) tends to argue against the climatic restriction hypothesis, as does the wide range of environments *A. ptyoptera* occupies within the "gorse area".

However, it may well be that the variation in host use by *A. ptyoptera* is a reflection of some other constituent of the environment unique to Canterbury & Otago.

The other possible cause for the geographic variation in host plant use is regional differences in the host plant. If this were the cause of the regionally restricted host shift, this would probably be related to the environmental differences noted above; however, in this study regional differences in gorse were not examined.

Because this issue is of such critical importance to the use of *A. ptyoptera* as a biocontrol agent, the above hypotheses should be tested. A simple experiment that would probably indicate the mechanism of this host shift would be to inoculate gorse plants in regions outside of Canterbury and Otago with *A. ptyoptera* individuals from gorse. The threat to *Carmichaelia* in these other regions posed by an expanding *A. ptyoptera* population may be avoided by confining the introduced moths to secure field cages.

The distribution of host use aside, the known overall range of *A. ptyoptera* is extensive. This widespread distribution includes: sub-tropical Auckland; relatively mild Marlborough and Hawkes Bay; high rainfall

West Coast; temperate Canterbury, Otago and Fiordland; and the harsh environment of the Tongariro Plateau. Although it is unknown if the distribution of *A. ptyoptera* is continuous between these areas, the almost nationwide distribution suggests it is a species tolerant of a wide variety of climates. Since gorse occupies a large variety of habits (see Section 2.3), such wide environmental tolerance is especially desirable. Further, the widespread distribution may favour the probability of establishment (Crawley 1987).

Another attribute of successful invaders is numerical abundance in their place of origin (Crawley 1986, 1987). Given the relatively few collection records for *A. ptyoptera*, it is unlikely that it achieves high numbers throughout its range (although its low rate of collection maybe due to a reluctance to fly to light traps). However, in mid-Canterbury it is at least "common" and usually "abundant". A similar pattern appears to occur in South Canterbury and parts of North Canterbury. Therefore the abundance of *A. ptyoptera* in Canterbury (and possibly Otago) relative to other areas is probably a function of its use of the very abundant gorse as a host plant.

### 5.5.4 Sub-Section Summary

Although elaborate procedures for eco-climatic matching the original range to the region of introduction may not be warranted, at least a reasonably close climatic match is almost certainly essential. In order to make a climatic match it is necessary to examine a biocontrol candidate's natural distribution. Another reason for this examination is that the range of habitats a candidate occupies is taken as indication of its ecological tolerances and adaptability.

*A. ptyoptera*, like its original host plants, is restricted to New Zealand. Collection records indicate that *A. ptyoptera* occurs throughout most of New Zealand. However, an incomplete search of New Zealand has shown that the *A. ptyoptera*-gorse association is restricted to some eastern parts of the South Island. It is suggested that this geographic divergence in host use warrants closer examination.

If subsequent experiments indicate that *A. ptyoptera* can infest gorse outside Canterbury and Otago, both positive and negative implications are raised for the use of *A. ptyoptera* as a biocontrol agent.

If the *A. ptyoptera*-gorse association cannot be transferred to other parts of New Zealand, then the application of *A. ptyoptera* will be restricted to places with environments similar to Canterbury and Otago and the potential value of the insect as a biocontrol agent will be diminished.

On the other hand, if the association can be transferred, the widespread distribution of *A. ptyoptera* indicates that it is a widely tolerant and adaptable species. However, the transfer of the *A. ptyoptera*-gorse association will support the possibility that the host shift has occurred *via* a genetic change and the ability to shift hosts may be maintained as part of the gene pool.

# *SECTION VI: Summary and Conclusions*

*A. ptyoptera* is a stem boring gelechiid that is endemic to New Zealand. It has successfully colonised the introduced weed gorse, and has been identified as a potential biocontrol agent of this weed.

Hill (1982) suggested that because gorse is a low quality food source, the 'prospects for control of *Ulex europaeus* by insects seem less than hopeful.' Nevertheless, New Zealand and Hawaii (and other countries) have active entomological gorse control programmes (Hill 1987; Markin & Yoshioka in press). As part of the Hawaiian State Department of Agriculture gorse control programme, aspects of the biology of *A. ptyoptera* and its potential as a biocontrol agent have been investigated in New Zealand.

The areas investigated in this work follow the standard principles of weed biocontrol, except that the *A. ptyoptera*-gorse association is a "new" one (*sensu* Hokkanen & Pimmentel 1984, 1989). The data collected in the course of this study have been discussed and presented in summary form at the end of each appropriate sub-section.

The execution and conclusion of many of the experiments within this work have been hindered by the growth form of gorse, and by the internal stem mining habit and the diffuse and complex life history of *A. ptyoptera*. Nevertheless a fairly detailed outline of the moth's natural history has been established. Details of the moth's biology can be combined with the areas examined in Section V to give a reasonably comprehensive estimate of the potential of *A. ptyoptera* as a biocontrol agent, before host specificity screening.

With regard to the potential of *A. ptyoptera* as a biocontrol agent, the attributes investigated are both positive and negative.

i) The direct damage caused by *A. ptyoptera* larval feeding can be very destructive, although the mean foliage loss of all plants was only between 10 and 14 percent. The indirect damage of *A. ptyoptera* appears to reduce the reproductive potential of gorse, and may contribute to the break-up and deterioration of gorse bushes.

ii) The seasonal life history of *A. ptyoptera* appears to be loosely structured univoltinism. The lack of structure, combined with evidence from the instar determination and the occurrence of two adult size groups, suggest that the life history (of *A. ptyoptera*) is very flexible. This flexibility results in larval attack continuing at all times of the year, and is likely to facilitate introduction and establishment in other countries.

iii) Compared with most gorse feeding insects, the reproductive potential of *A. ptyoptera* is very good. In Canterbury and possibly other parts of the South Island, the moth is at least common and usually abundant, despite 33-49 percent parasitism of the larvae.

iv) The immature life stages of *A. ptyoptera* do not seem susceptible to generalist mortality agents. Two undescribed species of larval parasitoid have been isolated: an endemic eulophid (*Zealachertus* sp.) and an ichneumonid (*Diadegma* sp.). As these parasitoids appear to be restricted to New Zealand, the potential for *A. ptyoptera* to achieve high population levels outside New Zealand appears favourable.

v) Although rearing larvae on general purpose artificial diet (Singh 1983) was not reliable, the results from this effort indicate artificial culturing of *A. ptyoptera* can be achieved.

vi) *A. ptyoptera* occurs throughout most of New Zealand and in a wide range of habitat types. This widespread distribution is taken as an indication of wide ecological tolerance. However, the *A. ptyoptera*-gorse association has only been found in some eastern parts of the South Island. Possible explanations for this geographical divergence in host plant use include:
a) This association is a function of some environmental feature unique to Canterbury and Otago, and so the association does not occur elsewhere. If this is the cause of the restriction of the *A. ptyoptera*-gorse association to these regions, the potential of *A. ptyoptera* as a biocontrol agent will be limited.
b) Only in Canterbury-Otago has the *A. ptyoptera* population developed the ability to exploit gorse. One of the many possible mechanisms by which such a host shift may have arisen is through genetic variation by the shifted population. If this is the case, the ability to shift hosts may be maintained.

vii) *A. ptyoptera* is an oligophagous species. The confirmed hosts of the moth occur within distinct tribes. This fact, and the possibility that *A.ptyoptera* has genetically maintained the ability to shift hosts, probably necessitates a cautious interpretation of host specificity screening results.

viii) Techniques suitable for host specificity screening have been developed. Although small arena oviposition testing proved problematic, the results indicate that *A. ptyoptera* females can discriminate in small cages. Neonate larvae starvation tests are probably the most reliable method of examining the host specificity of *A. ptyoptera*. However, without defining the mechanism(s) by which the *A. ptyoptera*-gorse association arose, the potential safety of the moth will probably remain unknown.

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# *APPENDIX I: SOLUTIONS*

## I.1 Heinz Mounting Medium

10g Poly Vinyl Alcohol (PVA)

40-60 mls Distilled water

10mls Glycerol

25mls Phenol/distilled water soln. (1.5%)

100g Chloral hydrate

35mls actic acid (85-92%)

**Method**

1) Add water to PVA powder, stirring constantly, the mixture being heated in a water bath at just below boiling.

2) Add lactic acid and stir for a few minutes.

3) add glycerol and stir till smooth.

4) Cool until luke-warm and add the chloral hydrate which has been preiously dissolved in the phenol solution.

5) Stir thoroughly and filter through and filter paper in a suction funnel.

6) Store in a brown bottle

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## II.2 Chlorazol Black E. Stain

'A good chitin stain, described by Cannon (*Nature*, 1937, **134:** 549). best used as a saturated solution in 70% alcohol. May be differentiated with terpineol if overstained' (Wagstaffe & Fidler 1955 pp168).

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## III.3 Carnoy's Fluid

Ethanol (95%) 6 parts
Chloroform 3 parts
Glacial Acetic Acid 1 parts

A fixitive for Lepidoptera larvae. Larvae can be left in this preservative overnight and then transferred to 75% alcohol. If instant preservation is required, the liquid can be heated (under a hot tap), poured off, and the specimen transferred to 75% alcohol.

# *APPENDIX II: HEAD-CAPSULE WIDTH INFORMATION*

## APPENDIX TABLE II.1: Head-capsule widths of *A. ptyoptera* larvae.

| SIZE (grat.units) | Total freq | Burnham 1988 | Field data Jan-Feb | Field data Mar-Apr | Jan-Feb | Mar-Apr | May-Jun | Jul-Aug | Sep-Oct | Nov-Dec |
|---|---|---|---|---|---|---|---|---|---|---|
| 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 21 | 0 | 14 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 49 | 1 | 43 | 6 | 2 | 1 | 0 | 0 | 0 | 0 |
| 11 | 4 | 0 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 12 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 13 | 15 | 5 | 6 | 4 | 4 | 1 | 0 | 4 | 0 | 1 |
| 14 | 6 | 2 | 3 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| 15 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| 16 | 7 | 3 | 0 | 1 | 0 | 1 | 2 | 4 | 0 | 0 |
| 17 | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 0 |
| 18 | 10 | 5 | 1 | 1 | 1 | 1 | 3 | 4 | 0 | 1 |
| 19 | 19 | 10 | 3 | 2 | 3 | 2 | 6 | 4 | 3 | 1 |
| 20 | 11 | 8 | 0 | 1 | 0 | 1 | 4 | 6 | 0 | 0 |
| 21 | 10 | 6 | 0 | 4 | 0 | 4 | 3 | 2 | 2 | 0 |
| 22 | 6 | 2 | 0 | 0 | 0 | 0 | 2 | 4 | 0 | 0 |
| 23 | 10 | 8 | 2 | 0 | 2 | 0 | 2 | 5 | 0 | 1 |
| 24 | 11 | 8 | 0 | 1 | 0 | 1 | 0 | 6 | 4 | 0 |
| 25 | 11 | 7 | 1 | 5 | 1 | 5 | 3 | 0 | 1 | 1 |
| 26 | 11 | 3 | 1 | 2 | 1 | 2 | 1 | 2 | 4 | 0 |
| 27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 28 | 10 | 7 | 0 | 0 | 0 | 0 | 4 | 4 | 1 | 1 |
| 29 | 9 | 8 | 0 | 1 | 0 | 1 | 3 | 2 | 2 | 0 |
| 30 | 11 | 5 | 2 | 2 | 2 | 2 | 3 | 3 | 0 | 1 |
| 31 | 6 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 3 |
| 32 | 9 | 5 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 2 |
| 33 | 3 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 |
| 34 | 12 | 8 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 6 |
| 35 | 8 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 1 |
| 36 | 6 | 5 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 3 |
| 37 | 10 | 6 | 0 | 2 | 0 | 2 | 1 | 0 | 3 | 4 |
| 38 | 15 | 6 | 2 | 1 | 2 | 1 | 2 | 2 | 4 | 4 |
| 39 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 40 | 15 | 4 | 1 | 0 | 1 | 0 | 3 | 2 | 4 | 6 |
| 41 | 6 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 |
| 42 | 13 | 5 | 1 | 1 | 1 | 1 | 4 | 0 | 1 | 6 |
| 43 | 7 | 3 | 2 | 0 | 2 | 0 | 1 | 1 | 1 | 1 |
| 44 | 17 | 7 | 3 | 0 | 3 | 0 | 0 | 2 | 4 | 9 |
| 45 | 3 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| 46 | 8 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 4 |
| 47 | 8 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 3 | 3 |
| 48 | 6 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 0 |
| 49 | 11 | 3 | 3 | 0 | 3 | 0 | 0 | 2 | 2 | 5 |
| 50 | 9 | 3 | 1 | 0 | 1 | 0 | 1 | 2 | 3 | 2 |
| 51 | 7 | 3 | 0 | 1 | 0 | 1 | 2 | 1 | 2 | 1 |
| 52 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 53 | 12 | 6 | 4 | 1 | 4 | 1 | 2 | 1 | 2 | 2 |
| 54 | 6 | 3 | 1 | 0 | 1 | 0 | 3 | 0 | 1 | 1 |
| 55 | 4 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| 56 | 8 | 3 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 2 |
| 57 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| 58 | 4 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 |
| 59 | 11 | 4 | 0 | 2 | 0 | 2 | 0 | 1 | 5 | 2 |
| 60 | 12 | 2 | 0 | 0 | 0 | 0 | 3 | 2 | 6 | 0 |
| 61 | 5 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 2 |
| 62 | 5 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 4 | 1 |
| 63 | 9 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 3 | 1 |
| 64 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 66 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 67 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 68 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 69 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 70 | 4 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 |
| 71 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 72 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 73 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 74 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 75 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 76 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**APPENDIX TABLE II.2: Head-capsule width frequencies used to calculate mean head-capsule widths of instar I & II.**

| SIZE (grat. units) | Frequency |
|---|---|
| INSTAR I | |
| 8 | 1 |
| 9 | 21 |
| 10 | 49 |
| 11 | 4 |
| INSTAR II | |
| 12 | 1 |
| 13 | 15 |
| 14 | 6 |
| 15 | 3 |
| 16 | 1 |

# *APPENDIX III: SEASONAL DISRIBUTION OF LIFE STAGES AND ARTIFICIAL REARING DATA*

## APPENDIX TABLE III.1: Collection record information, field monitoring and larvae data

MONTH: January SEASON: Summer

**COLLECTION RECORD DATA**

| Life history stages: | Adults (2) | Adults (7) | Adults (7) | Adults (10) | Adults (3) |
|---|---|---|---|---|---|
| Location: | Christchurch MC, N.ZL. | Franz Joseph WD & ChCh. | ChCh, MC & Waiho, WD | Lincoln & Ch Ch, MC | Various, DN |
| Date: | 1927, 1988 | 1925 (5); 1927 (2) | 1922, 23, 27 33; 22, 24 | 1964, 65, 68 | 1979, 85 |
| Collector: | Unknown, J.S. Dugdale | Clarke Coll. -Auckland | Various | Various | Brian Patrick |
| Source: | National Arth. Coll. | War Mem. Museum & Inst. | National Mus. of N.Z. | Lincoln Uni. Museum | Collection |

**FIELD MONITORING DATA**
Life history stages present: egg, larva, pupa, adult

Parasite particulars : *Diadegma* sp. cocoon and adult; recently emerged *Zealachertus* sp. pupal cases and adults

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | - | 46 | 12 |
| Mean head capsule width: | - | 24.8 | 23.3 |
| Range: | - | 8-54 | 10-50 |
| Standard deviation: | - | 16.39 | 15.66 |
| Standard error: | - | 2.42 | 4.52 |

OTHER INFORMATION: Current seasons pupal cases present. Therefore emerged before January

MONTH: February SEASON: Summer

**COLLECTION RECORD DATA**

| Life history stages: | Adult (2) | Adult | Adult | Adult (4) | Larva |
|---|---|---|---|---|---|
| Location: | Dart R. OL, Laingholm AK | Mt. Gra ? | Waiho Gorge WD | Enfield DN; Alexandra CO | Loburn NC; Palmerston DN |
| Date: | 1980; 1980 | 1917 | 1920 | 1978, 79; 1984 | 1972; 1984 |
| Collector: | K.J. Fox; R. Kleinpaste | Clarke Coll. -Auck. War | S. Lindsay-G.V. Hudson | Brian Patrick | Unknown |
| Source: | Nat. Arth. Coll. | Mem. Mus. & Institute | Coll.- Nat. Museum NZ | Coll. | MAF(Lincoln) Spirit Coll. |

**FIELD MONITORING DATA**
Life history stages present : egg, larva, pupa? adult

Parasite particulars: *Diadegma* sp. cocoon, recently emerged cocoon and adult

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | - | 48 | - |
| Mean head capsule width: | - | 13.23 | - |
| Range: | - | 9-56 | - |
| Standard deviation: | - | 10.2 | - |
| Standard error: | - | 1.47 | - |

OTHER INFORMATION: Small field sample of larvae - mostly lab. reared

MONTH: March SEASON: Summer/ Autumn

**COLLECTION RECORD DATA**

| | | | | | |
|---|---|---|---|---|---|
| Life history stages: | Adult (2) | Adult | Adult (2) | | |
| Location: | Laingholm AK | Christchurch MC | Dunedin DN | | |
| Date: | 1980 | 1982 | 1983 | | |
| Collector: | R. Klein-paste | C.A. Muir | Brian Patrick | | |
| Source: | Nat. Arth. Coll. | Lincoln Uni. Museum | Coll. | | |

**FIELD MONITORING DATA**
Life history stages present: egg, larva, adult

Parasite particulars :

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | - | 15 | - |
| Mean head capsule width: | - | 9.9 | - |
| Range: | - | 9-13 | - |
| Standard deviation: | - | 1.33 | - |
| Standard error: | - | 0.34 | - |

OTHER INFORMATION: Larvae sample all lab. reared - no field samples recovered. Current seasons damage first noticed (1988)

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MONTH:April SEASON: Autumn

**COLLECTION RECORD DATA**

| | | | | | |
|---|---|---|---|---|---|
| Life history stages: | Adult | Larvae | | | |
| Location: | Christchurch MC | Leeston MC | | | |
| Date: | 1983 | 1979 | | | |
| Collector: | C.A. Muir | Unknown | | | |
| Source: | Lincoln Uni. Museum | MAF(Lincoln) Spirit Coll. | | | |

**FIELD MONITORING DATA**
Life history stages present: larva

Parasite particulars: *Zealachertus* sp. pupa recovered.

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | - | 38 | - |
| Mean head capsule width: | - | 33.3 | - |
| Range: | - | 13-69 | - |
| Standard deviation: | - | 15.8 | - |
| Standard error: | - | 2.56 | - |

OTHER INFORMATION:

MONTH: May SEASON: Autumn

**COLLECTION RECORD DATA**

| | | | | | |
|---|---|---|---|---|---|
| Life history stages: | Adult | | | | |
| Location: | Reefton Saddle BR | | | | |
| Date: | 1962 | | | | |
| Collector: | Unknown | | | | |
| Source: | FRI Insect Coll. | | | | |

**FIELD MONITORING DATA**
Life history stages present : larva

Parasite particulars : Emerged *Diadegma* sp. cocoons recovered

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | - | 26 | - |
| Mean head capsule width: | - | 41.65 | - |
| Range: | - | 19-60 | - |
| Standard deviation: | - | 13.95 | - |
| Standard error: | - | 2.74 | - |

OTHER INFORMATION:

---

MONTH: June SEASON:Winter

**COLLECTION RECORD DATA**

| | | | | | |
|---|---|---|---|---|---|
| Life history stages: | | | | | |
| Location: | | | | | |
| Date: | | | | | |
| Collector: | | | | | |
| Source: | | | | | |

**FIELD MONITORING DATA**
Life history stages present: Larva

Parasite particulars : Recently? emerged *Diadegma* sp. cocoon

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | - | 56 | - |
| Mean head capsule width: | - | 33.95 | - |
| Range: | - | 16-70 | - |
| Standard deviation: | - | 15.58 | - |
| Standard error: | - | 2.08 | - |

OTHER INFORMATION:

MONTH: July SEASON: Winter

**COLLECTION RECORD DATA**

| | | | | | |
|---|---|---|---|---|---|
| Life history stages: | | | | | |
| Location: | | | | | |
| Date: | | | | | |
| Collector: | | | | | |
| Source: | | | | | |

**FIELD MONITORING DATA**

Life history stages present : Larva

Parasite particulars : *Zealachertus* sp. pupa; Unknown brachonid or ichneumonid cocoon

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | - | 53 | - |
| Mean head capsule width: | - | 32.58 | - |
| Range: | - | 13-66 | - |
| Standard deviation: | - | 15.76 | - |
| Standard error: | - | 2.14 | - |

OTHER INFORMATION:

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MONTH: August SEASON: Winter

**COLLECTION RECORD DATA**

| | | | | | |
|---|---|---|---|---|---|
| Life history stages: | | | | | |
| Location: | | | | | |
| Date: | | | | | |
| Collector: | | | | | |
| Source: | | | | | |

**FIELD MONITORING DATA**

Life history stages present: Larva

Parasite particulars : *Diadegma* sp. cocoon (pupal)

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | | 37 | |
| Mean head capsule width: | | 27.86 | |
| Range: | | 12-63 | |
| Standard deviation: | | 14.12 | |
| Standard error: | | 2.32 | |

OTHER INFORMATION: Possible recently emerged pupal cases - early emergence.

MONTH: September SEASON: Spring

**COLLECTION RECORD DATA**

| | | | | | |
|---|---|---|---|---|---|
| Life history stages: | | | | | |
| Location: | | | | | |
| Date: | | | | | |
| Collector: | | | | | |
| Source: | | | | | |

**FIELD MONITORING DATA**

Life history stages present : larva, prepupal larva

Parasite particulars : Unknown Ichneumonid or brachonid cocoon found; *Diadegma* sp. cocoon and adult; *Zealachertus* adults (in gallery)

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | 5 | 37 | - |
| Mean head capsule width: | 46.8 | 40.22 | |
| Range: | 25-75 | 15-61 | - |
| Standard deviation: | 24.37 | 12.5 | - |
| Standard error: | 10.9 | 2.05 | - |

OTHER INFORMATION:

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MONTH: October SEASON:Spring

**COLLECTION RECORD DATA**

| | | | | | |
|---|---|---|---|---|---|
| Life history stages: | Adult | Larva | | | |
| Location: | ChCh MC | Southbridge MC | | | |
| Date: | 1924 | 1980 | | | |
| Collector: | Unknown | Unknown | | | |
| Source: | Nat. Arth. Coll. | MAF(Lincoln) Spirit Coll. | | | |

**FIELD MONITORING DATA**

Life history stages present : larva, prepupal larva

Parasite particulars : *Diadegma* sp. pupal cocoon

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | 10 | 44 | - |
| Mean head capsule width: | 38.5 | 48.15 | - |
| Range: | 17-62 | 19-70 | - |
| Standard deviation: | 14.53 | 12.77 | - |
| Standard error: | 4.59 | 1.93 | - |

OTHER INFORMATION:

MONTH: November SEASON: Late spring

**COLLECTION RECORD DATA**

| Life history stages: | Adult | Adult | Adult | Adult | Larva |
|---|---|---|---|---|---|
| Location: | Prices Bush MC | Lincoln MC | Dessert Rd. TO | Enfield DN | Rakaia Gorge MC |
| Date: | 1933 | 1968 | 1958 | 1978 | 1978 |
| Collector: | White Coll.- National | Unknown | Unknown | Brian Patrick | Unknown |
| Source: | Museum of New Zealand | Lincoln Uni. Museum. | FRI Insect Coll. | Collection | MAF(Lincoln) Spirit Coll. |

**FIELD MONITORING DATA**
Life history stages present: larvae, prepupal larva, pupa, adult

Parasite particulars: *Diadegma* adult

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | 37 | 12 | - |
| Mean head capsule width: | 43.05 | 39.5 | - |
| Range: | 31-64 | 18-58 | - |
| Standard deviation: | 9.16 | 12.51 | - |
| Standard error: | 1.51 | 3.61 | - |

OTHER INFORMATION:

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MONTH: December SEASON: Summer

**COLLECTION RECORD DATA**

| Life history stages: | Adult (2) | Adult | Adult (3) | Adult (2) | Adult (2) |
|---|---|---|---|---|---|
| Location: | Burwood MC; Hawkes B. HB | ChCh, MC | Lincoln MC ChCh MC | Eyrewell MC | Enfield DN Deep Cove FD |
| Date: | 1925; 1969 | 1919 | 1967, 68; 1983, 81 | 1964 | 1978; 1985 |
| Collector: | Unknown; T.W. Davies | Clarke Coll- Auck. War | Unknown;C.A. Muir,J.Early | Unknown | Brian Patrick |
| Source: | Nat. Arth. Coll. | Mem. Mus. & Institute | Lincoln Uni. Museum | FRI Insect Coll. | Collection |

**FIELD MONITORING DATA**
Life history stages present : egg, larva, prepupal larva, pupa

Parasite particulars : Parasite (*Diadegma*) larva dissected from *A. ptyoptera* larva; *Zealachertus* sp. pupa.

**LARVAE DATA**

| | 1987 | 1988 | 1989 |
|---|---|---|---|
| Sample size: | 23 | 14 | - |
| Mean head capsule width: | 45 | 42 | - |
| Range: | 30-56 | 13-66 | - |
| Standard deviation: | 7.9 | 15.85 | - |
| Standard error: | 1.65 | 4.24 | - |

OTHER INFORMATION: Parasitised larva (moribund) noticed

## APPENDIX TABLE III.2: Results from 1988-1989 diet trial

**Larval Size: Large**

| | Dates | | | |
|---|---|---|---|---|
| Larvae | Start | Death | Emergence | Comments |
| 1 | 27/8/88 | | 1/11/88 | Pupated 10/10.Emerge Deformed |
| 2 | 27/8/88 | | 1/11/88 | Deformed and small |
| 3 | 29/8/88 | | 28/11/88 | Pupa 1/11. Large |
| 4 | 29/8/88 | | 14/11/88 | Pupa 1/11. Diet mouldy twice |
| 5 | 29/8/88 | 6/11/88 | | Diet dehydrated. Fail to pupa |
| 6 | 29/8/88 | | 14/11/88 | Pupa 1/11. Diet mouldy. Small |
| 7 | 29/8/88 | 1/11/88 | | Diadegma parasite (em. 14/11) |
| 8 | 29/8/88 | | 20/12/88 | Deformed & small. Died 23/12 |
| 9 | 29/8/88 | 13/11/88 | | Diet dehydrated.Didn't pupate |
| 10 | 29/8/88 | 7/9/88 | | Injured on collection? |
| 11 | 29/8/88 | ?/1/89 | | Pupa 14/11.Mouldy- Fail to em |
| 12 | 29/8/88 | | 28/11/88 | Pupa 1/11. Large |
| 13 | 29/8/88 | 1/11/88 | | Killed in transit from mould |
| 14 | 29/8/88 | 14/11/88 | | Diet mouldy. Fail to pupate |

**Larval Size: Medium**

| | Dates | | | |
|---|---|---|---|---|
| Larvae | Start | Death | Emergence | Comments |
| 1 | 27/8/88 | | 20/12/88 | Pupa 28/11. Small |
| 2 | 27/8/88 | ?/9-10/88 | | Fail to estb. Diet too moist? |
| 3 | 27/8/88 | 7/9/88 | | Injured on collection |
| 4 | 29/8/88 | 22/9/88 | | Diet mouldy. Fail to pupate |
| 5 | 29/8/88 | | 28/11/88 | Pupa 1/11. Large |
| 6 | 29/8/88 | 7/9/88 | | Injured on collection |
| 7 | 29/8/88 | | 28/11/88 | Pupa 14/11.Large.Diet mouldx2 |
| 8 | 29/8/88 | | 28/11/88 | Deformed. Died soon after em. |
| 9 | 29/8/88 | 7/9/88 | | Fail to estb. Diet too moist? |
| 10 | 29/8/88 | ?/9-10/88 | | Fail to estb. Diet too moist? |
| 11 | 29/8/88 | 4/10/88 | | Diet mouldy. Transfered x 1 |
| 12 | 29/8/88 | 28/11/88 | | Diet dehydrated.Didn't pupate |
| 13 | 29/8/88 | 1/11/88 | | Diadegma parasite (em. 28/11) |
| 14 | 29/8/88 | | 28/11/88 | Pupa 1/11. Large |
| 15 | 29/8/88 | | 12/12/88 | Pupa 28/11. Small.Diet mouldy |
| 16 | 29/8/88 | 1/11/88 | | Diet dehydrated.Didn't pupate |
| 17 | 29/8/88 | 17/10/88 | | Diet mouldy. Transfered x 2 |
| 18 | 29/8/88 | 22/9/88 | | Diadegma parasite (em. 29/9) |
| 19 | 29/8/88 | ?/1/89 | | Fail to pupate.Diet mould x 2 |

**Larval Size: Small**

| | Dates | | | |
|---|---|---|---|---|
| Larvae | Start | Death | Emergence | Comments |
| 1 | 29/8/88 | ?/9-10/88 | | Fail to estb. Diet too moist? |
| 2 | 29/8/88 | 6/11/88 | | Diet dehydrated.Didn't pupate |
| 3 | 29/8/88 | 7/9/88 | | Not estb. Injured on coll? |
| 4 | 29/8/88 | ?/9-10/88 | | Fail to estb. Diet too moist? |
| 5 | 1/9/88 | | 12/12/88 | Pupa 28/11. Small |
| 6 | 1/9/88 | | 9/1/89 | Pupa 20/12. Diet Mouldy.Large |
| 7 | 1/9/88 | ?/9-10/88 | | Fail to estb. Diet too moist? |
| 8 | 1/9/88 | 10/10/88 | | Unknown para. (Didn't emerge) |

# *APPENDIX IV: Distribution of A. ptyoptera*

**APPENDIX TABLE IV.1: The distribution of *A. ptyoptera;* collection records and recoveries from gorse.**

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**Collection records, host unknown (i.e. adults collected):**
-Laingholm, West Auckland, AK (x3)
-Little Bush, Hawke's Bay, HB
-Mt Grey, NC
-Burwood, Christchuch, MC
-Spreydon, Christchuch, MC (x3)
-Sydenham, Christchurch, MC (x3)
-MacLeans Island, MC
-Defiance Hut (2600 ft), Franz Josef, WD (x5)
-Riccarton Bush, Christchuch, MC (x2)
-Dallington, Christchuch, MC (x2)
-Lincoln College, MC (x13)
-Reefton Saddle (500 ft), BR
-Waiho Gorge, WD (x2)
-Enfield, DN (x6)
-Dunedin, DN (x2)
-Mt Cargill (600 m), DN
-Portobello, DN
-Alexandra, CO
-Dart Hut, Near L. Wakatipu, OL
-Homer Tunnel (2500 ft), FD
-Deep Cove, FD
-Brooklands, Unknown
-Prices Bush, Unkwown

**Collection records, host known:**
-Desert Road, TO: ex *Carmichaelia* sp.
-Eyrewell, MC (x2): ex gorse
-Leeston, MC: ex gorse
-Southbridge, MC: ex gorse
-Lobum, NC: ex gorse
-Rakaia Gorge, MC ex gorse
-Palmerston, DN: ex *Clianthus puniceus*

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**Present on gorse:**
-Hinkswell Stream, KA
-Hinkswell Overbridge, KA
-Spotswood, NC
-Cheviot, NC
-Amberley, NC
-Lobum, NC
-Lake Grassmere,MC
-Cass, MC
-Porters Pass (bottom of), MC
-Sheffield, MC
-L. Coleridge, MC
-Glenroy, MC
-Greenpark, MC
-Springston, MC
-Coes Ford, MC
-Burnham, MC
-Dunsandel, MC
-Ashburton, MC
-Hinds, MC
-Rangitata, SC
-Cave, SC
-Pleasant Point, SC
-Orari Bridge, SC
-Geraldine, SC
-Alma, DN
-Pareora and environs, SC
-Maheno, DN
-Herbert, DN
-Ranfurly, CO
-Morrisons, CO
-Omakau, CO
-Roxbrough, CO
-Alexandra, CO
-Ettrick, CO

**Not found on gorse:**
-Waimate North, ND
-L. Omapere, ND
-Maraeroa, ND
-Kaikohe, ND
-Kawakawa, ND
-Nukutawhiti, ND
-Dargaville, ND
-Ruawai, ND
-Wellsford, AK
-Warkworth, AK
-Orewa, AK
-Greenhithe, AK
-Wellington and environs, WN
-Ruby Bay, NN
-Nelson, NN
-Stoke, NN
-Richmond, NN
-Havelock, SD
-Renwick, MB
-Rapaura, MB
-Bleinheim environs, MB
-Seddon, KA
-Dashwood, KA
-Kaikoura and environs, KA
-Conway River, KA
-Greymouth, BR
-Hokitiki, WD
-Kumara, WD
-Dillmanston, WD
-Jacksons, WD
-Temuka, SC
-Moeraki, DN
-Lawrence, DN
-Henley, DN
-Milton, DN
-Raes Junction, CO

*Space Cat Productions*

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